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With the assistance of other members of the botanical staff of the University of Chicago

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P. 57, line 10, for higher read lower

P. 181, footnote line 4, for FINDFUSZ read RINDFUSZ

P. 300, line 7, for even read do not even

P. 316, fig. 1, lowest filled circle of 1921 curve should be open circle of 1919 curve

VOLUME LXXIV NUMBER 4

THE
BOTANICAL GAZETTE

December 1922

ECOLOGICAL FACTORS IN REGION OF STARVED ROCK, ILLINOIS

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 299

FRANK THONE

(WITH FIVE FIGURES)

Introduction

The work of COWLES (5) in calling the attention of the then newly differentiated science of plant ecology to the concept of plant associations as stages in successions, not as entities complete and final in themselves, but rather as steps in the evolution of social life in the plant world, was of far reaching influence in determining the development of ecology in America as a dynamic science, as the study of a progress rather than as a mere set of methods for the description of states. COWLES was also the first to emphasize the importance of topography as a general control over other factors that directly influence the activities of plants.

The earlier work in this field contented itself with pointing out the general effects of topography as a modifier, within a given region, of the climatic factors. It indicated the direction of such modifications, but only estimated their extent; it was qualitative rather than quantitative. It was, however, only natural that as time passed students of ecology should desire to gain a more exact knowledge of the factors controlling plant communities and their development, and a good share of the work now being done in Ameri-

can and British ecology concerns itself with the measurement of such factors as soil moisture, soil chemistry, temperature of both soil and air, evaporating power of the air, and intensity of sunlight. With the cooperation of ecological plant physiologists, a number of more or less satisfactory methods for the measurement of these factors have been evolved. Among the many workers on the problems of soil moisture, BRIGGS and SHANTZ (3) may be cited for their development of the wilting coefficient concept, BRIGGS and MCLANE (2) for the moisture equivalent idea, ALWAY (1) for the hygroscopic coefficient, and LIVINGSTON and KOKETSU (11) for the invention of the so-called soil points. Thermometric data were among the earliest to be gathered, although they are still among the least satisfactorily interpreted; special citations appear to be superfluous. Exception might be claimed for the "life zone" idea best developed by MERRIAM (15), but this is regional-climatic rather than local and topographic.

Modern ecological work in the measurement of the evaporating power of the air dates chiefly from the re-invention and popularization by LIVINGSTON (8, 9) of the porous cup atmometer. From time to time numerous attempts have been made to develop photographic and other methods for a field study of sunlight intensity, but none of them has been very satisfactory to students of plant activities. PULLING (16) gives a concise review of the work in this field. About the only instrument at present used by anyone except its own inventor is LIVINGSTON'S radio-atmometer (10), which obtains an approximate measurement of the effect of direct solar radiation on evaporation from a free water surface. Other methods for the measurement of ecological factors have some local vogue, but those here outlined are the ones most frequently used.

So widespread has been the practice of factor measurement, and so many the workers, that a complete review of the literature would be impossible in this connection, and in view of the extensive literature cited in such standard works as those of LIVINGSTON and SHREVE (12), and of CLEMENTS (14), may well be omitted.

An important consideration in the development of a successional series, but one that is not always given the prominence it deserves, is the fact that the determining conditions that permit or bar the

entrance of new species in a given area are operative first on the seedling. Liminal conditions act on the infant of the race, practically always. The operation of this principle may be seen in the cultivation of adult plants outside of their natural habitats. These often thrive, but do not produce offspring. By the simple law of chance, propagules of all sorts are constantly falling into every area within the range of flight or carriage from the parent, but only where conditions are such as to permit their germination and initial growth do they become established. Once established they may weather an unfavorable season, but they cannot gain a foothold at all in a place where the conditions are unfavorable all the time. This principle recognized, it becomes at once apparent that any measurements undertaken with a view to their bearing upon succession should be made with special reference to seedling seasons and places. The first worker to use this idea as a definite basis for his investigations was FULLER (7), who made a study of the water relations of several plant associations on and near the Indiana dunes. His results indicated that the water supplying power of the soil was fairly uniform, or at least adequate for growth, throughout the season at all of his stations. On the other hand, the evaporating power of the air varied markedly, showing a pronounced correlation with the type of vegetation. The rate of evaporation bore an inverse relation to the density of the vegetation, being greatest on the cottonwood dune and least in the beech-maple forest. FULLER concluded that the differences in evaporation rates were sufficient to account for the successional range between the relative xerophytism of the cottonwood dune and the mesophytism of the climax forest.

The present problem

TERRAIN

Conditions rivalling those of the dunes in diversity of vegetational associations to be found within narrowly restricted limits exist in numerous steep-sided river gorges and their associated canyons scattered across the whole Mississippi Valley, along the edges of the various glacial drift areas, and in the unglaciated areas adjoining them. These cliffs and canyons are invariably the

habitats of disjunct groups of various kinds: glacial relicts left behind by the northern retreat of the first post-Pleistocene flora, outliers from the mesophytic southeastern forests, forerunners of western and southwestern plains, and desert types. This contact of outposts of such different plant hosts is in itself an argument for the existence of notably different environmental complexes in close juxtaposition, and hence for the advantageousness of such locations as critical points in the study of the physical factors of ecology.

The data for the present study were obtained at the Illinois State Park at Starved Rock, in La Salle County, Illinois. Here, during early post-glacial times, the Illinois River cut a steep-sided trench through the St. Peter sandstone (which at this point is thrust to the surface by the La Salle anticline), and through its overlying strata of Pottsville shales and clays and blanket of glacial till. The geography of this region has been treated in detail by SAUER, and the geology by CADY (6). The sides of the trench still remain as lines of steep cliff, about a mile apart, facing each other across the floodplain of the now much shrunken river. The cliff on the south side of the river, from a point opposite the village of Utica eastward for about seven miles, is unusually precipitous and high, reaching a maximum of 157 feet from crest to mean low water level at the Starved Rock itself. It is furthermore cut into by a series of remarkable box canyons made by small tributary streams. Their sides are as precipitous as those of the cliff itself, and for the most part their bottoms are either at or near base level. Since the recession of the river (which now washes the base of the cliff only in a few limited spots, notably Starved Rock, Lovers' Leap, and Pulpit Rock) erosional débris has collected in places as talus slopes at the foot of the cliff, both within and outside the canyons. In addition, there are at the top of the cliffs the steep slopes from the top of the sandstone caprock to the general level of the upland till, and at the base a number of fragmentary river terraces of varying age, including oxbows in various stages of filling, and finally the present juvenile (and largely treeless) floodplain. A cross-section through a typical location either over the cliff side or into a canyon, therefore, would reveal the following types of terrain: (1) level upland of glacial or Pottsville clay; (2) more or less steep slope toward the edge of

the sandstone cliff, also clayey; (3) exposed edge of cliff, sandy or sand mixed with clay and shale; (4) precipitous cliff, usually with weathered crevices and shelves; (5) talus slope, generally very sandy, with much humus and some clay; (6) canyon bottom (alluvial), or river terrace (alluvial to sandy), or juvenile floodplain (alluvial).

VEGETATION

With so varied a terrain as that just outlined, presenting such widely diverse types of habitat, it is only natural to expect a very widely diversified vegetational development. This expectation is well realized, for within the limits of the scant thousand acres of the Starved Rock State Park there is a collection of plants that for floristic and ecological interest can hardly be matched. All the orthodox successional stages between *Quercus macrocarpa* of the prairie edges and *Q. velutina* of the upland woods, to *Q. bicolor* of the sloughs and the *Populus-Salix* thickets of the river edge are there as a matter of course; but the region offers all the groups of disjuncts mentioned in a preceding paragraph as well. There are places in this park where one can stand beside a white pine and throw a stone through the top of a pawpaw!

No attempt can be made in this place even to outline the vegetational types to be found in this region. This has been presented briefly by COWLES (**6**), and a more detailed description by the present writer is now in preparation. The present study concerns itself more with the physical factors of the environment, especially as they affect seedling growth and hence succession, in a number of typical locations in the park. Ideally these determinations should have been made in a considerable number of places, at least three for each clearly distinguishable type of association, but this was beyond the available resources in time and apparatus. In all, seven stations were maintained throughout the major portion of one growing season, two on the upland, three on talus slopes, and two at the bottom. In locating these, some diversity was possible, overcoming in at least a slight degree the unavoidable inadequacy of data. Stations 7 and 6 were located on the upland, no. 7 on the upland proper, in a second growth *Quercus velutina-Q. alba-Carya ovata* association, and no. 6 on a gentle slope from this toward the edge

of the cliff (but away from the exposed sandy terrain), in a second growth *Quercus rubra-Q. alba* association, with considerable undergrowth of *Cornus*, *Viburnum*, and seedlings of *Prunus*, etc. Stations 5, 3, and 2 were located on talus slopes, no. 5 about one-third of the way down one, on the face of the cliff, and nos. 3 and 2 near the tops of slopes on opposite sides of Hennepin Canyon. The tree growth at station 5 was predominantly *Quercus rubra*, with some *Q. alba*, *Juglans cinerea*, and *Tilia americana*, and a scattering of other mesophytic hardwood species. The shrubby undergrowth consisted mostly of *Hamamelis virginiana*, and the herbaceous situation was dominated by a magnificent "fernery" of *Osmunda claytoniana*. The soil here was a sand rich in humus, but with little clay. Station 3, within the canyon, was on a rather newer slope, the soil containing a considerable proportion of clay. The tree growth consisted largely of *Prunus serotina*, and there was a dense undergrowth of *Psedera quinquefolia*, *Ribes cynosbati*, *Lonicera Sullivantii*, and *Hydrangea arborescens*. There was also a fair development of mesophytic herbs. Station 2 was on a slope that was newer still. The soil was sandier than on station 3, but raw and poor in humus. It was full of stones, with large, moss-covered rocks protruding. There were fewer trees, and these were mostly young and small. A very considerable growth of *Hamamelis virginiana* was present, but few other shrubs, and almost no herbs. These three stations represented fairly well the state of the more mesophytic talus slopes. Stations 4 and 1 were on representative bottomlands, no. 4 being on the river floodplain and no. 1 on the floor of the canyon. The soil in both places was a black alluvium. The association at station 4 was dominated by *Acer saccharinum* and *Ulmus americana*, with many seedlings and saplings. Other undergrowth was mostly herbaceous, with *Laportea canadensis*, *Boehmeria cylindrica*, and *Campanula americana* as the conspicuous species. The alluvial floor of the canyon, where station 1 was located, bore an association of *Ulmus*, with some admixture of *Juglans*, *Fraxinus*, *Populus*, *Salix*, etc. Seedlings and young trees were numerous, and there was a fair amount of undergrowth, consisting largely of *Sambucus canadensis*, and at one place a notable thicket of *Euonymus*. There was an exceedingly rich, moist-

mesophytic herbaceous flora, typified by *Impatiens pallida*, *Pilea pumila*, *Campanula americana*, and *Lobelia syphilitica*. Lianas were abundant, more so than at station 4. In general, this was by far the most mesophytic of all the stations. These three groups of stations were thus fairly typical of upland, slope, and bottomland respectively, and represented the principal plant associations reasonably well.

Instruments and methods

An effort was made at each station to secure some measurement of each of the following physical factors: soil moisture, evaporating power of the air, intensity of solar radiation (in terms of its effect on evaporation from a free water surface), and temperature of soil and air.

SOIL MOISTURE.—Soil moisture data were obtained by (1) the usual determination of the oven-dry weight percentage in samples of about 200 gm. each, compared with the wilting coefficients, as derived by the indirect method of BRIGGS and SHANTZ; and (2) the "soil point" method of LIVINGSTON and KOKETSU. All data were obtained for a level of approximately 7.5 cm. below the soil surface. This was the shallower of the two depths used by FULLER in his dune studies, and represents the level at which most seedlings begin their adventures. The soil points were used in sets of four, and results recorded as the average, to eliminate as far as possible the errors due to variability in instruments and soil. Holes were dug to the proper depth with a trowel, care being taken that none of them was within one-half meter of any hole in the same set or any previous set. As a rule, soil from the holes into which the points were set was taken for use in the moisture percentage determinations. From April 30 until July 1 it was possible to visit the stations only three or four times a month. From July 1 until September 20 determinations were made every forty-eight hours, except when rain intervened.

EVAPORATING POWER OF AIR AND SUNLIGHT INTENSITY.—Data on the evaporating power of the air and on the effect of direct solar radiation on evaporation rate were obtained by means of a pair of standard Livingston spherical atmometer cups at each station.

These were equipped with the rainproofing valves described by LIVINGSTON and THONE (13). Their reservoir bottles were partly buried, so that the cups were about 20 cm. above the ground level. From April 30 until July 1 readings were made weekly or fortnightly, during the month of July they were made daily, and from August 6 until September 20 they were made every two days. All readings, after correction, were reduced to mean daily rates for ten-day periods.

TEMPERATURE.—Air temperatures were obtained from a Six-type minimax thermometer at each station. The thermometers were placed at the same level as the atmometers. No artificial shelter was used except at station 1, since there was sufficient natural cover to protect the instruments from direct insolation at all the other stations, and even at the latter place the growth of the *Impatiens* thicket soon made artificial shelter unnecessary. Readings were made on the same schedule as that used in the atmometer observations. The stations were visited each day just before the period of maximum temperature, so that the maxima and minima for the preceding twenty-four or forty-eight hour period were obtained.

Soil temperatures were obtained by means of test-tubes sunk into the soil to a depth of 10 cm. The lower end was kept filled with water, and the tube kept stoppered. When an observation was to be made, a thermometer was lowered into the tube until the bulb was immersed in the water, and read after sufficient time had been allowed for an equilibrium to be reached. Since the readings were always made shortly before the period of maximum air temperature, it may be assumed that the soil temperatures thus obtained were a little below the maximum for the day. Since, however, the total diurnal fluctuations in soil temperatures are known to be small, and especially since in the present study they seemed in the end to have no particular significance, this source of inaccuracy, as well as the rather crude method employed for obtaining the data, may be overlooked.

For both air and soil temperatures, it may be remarked that the figures up to July 1 can have but little significance, since they apply to periods of seven or fourteen days. During July, of course, true

diurnal data were obtained. From August 6 until September 20 readings were made every forty-eight hours.

Discussion

SOIL MOISTURE (figs. 1, 2).—It is obvious that topography cannot affect the availability of soil water for plant growth until two other factors have operated. The first of these, the amount and distribution of precipitation, is climatic, and thus affects all locations about equally. The second factor (or more properly group of factors) is strictly edaphic, having to do with the effect of the mechanical makeup of the soil (size, arrangement, and packing of soil particles) upon the capacity of the soil to absorb and hold precipitation water, and to deliver it to the roots of the plants when they demand it. Finally, the topography is of importance in its effect upon such factors as run-off, subsurface drainage, and exposure to factors that influence evaporation, both from the surface of the soil itself and through plant transpiration.

The effects of the climatic factors are plainly evident in the general conformity of all the curves in the soil moisture graphs, both those representing the growth water (fig. 1) and those representing the results of the operation of the Livingston-Koketsu soil points (fig. 2). After the cessation of the spring rains in early June, and until their resumption in early September, the season was one of the hottest and driest summers on record in recent years. There was but one brief period of precipitation, heavy rains occurring during the first few days of August. The soil water percentages show a notable correlation between the rainfall distribution and the water content of the soil at all the stations. Beginning with moderate but varying amounts during the late spring rains, all stations showed a falling off throughout June, increasing in amount and rate of loss through the July drought, and ending in a sudden increase at the time of the early August rain. Following this was another sharp decrease throughout August, until a period of rains in early September brought a rise, somewhat resembling that of early August, but less in amount. Fair weather during the last observation period of the season brought the beginning of another decrease. The ready responses of the curve to both drought and rain are very notable features.

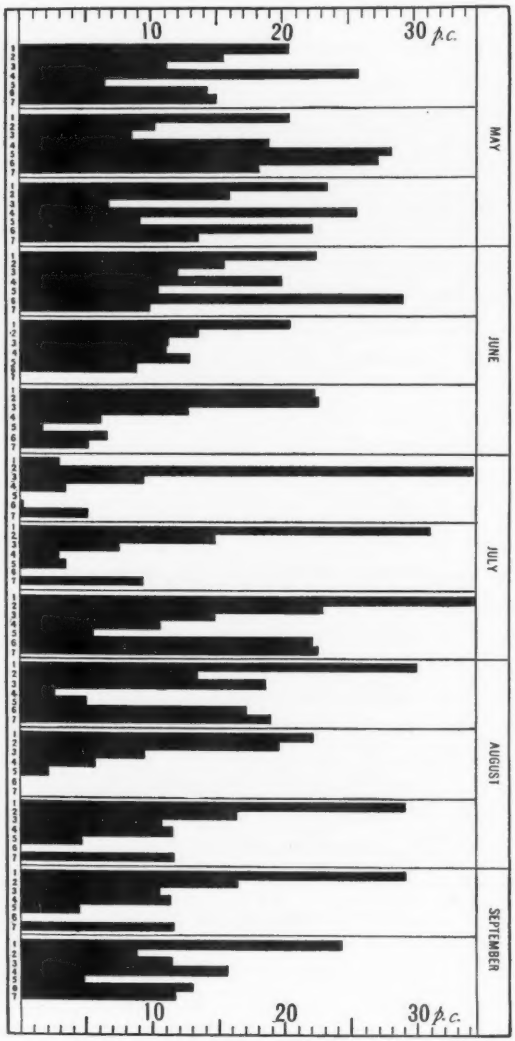

FIG. 1.—Percentages of growth water present in soil at seven representative stations, during ten-day periods from May 1 to September 20.

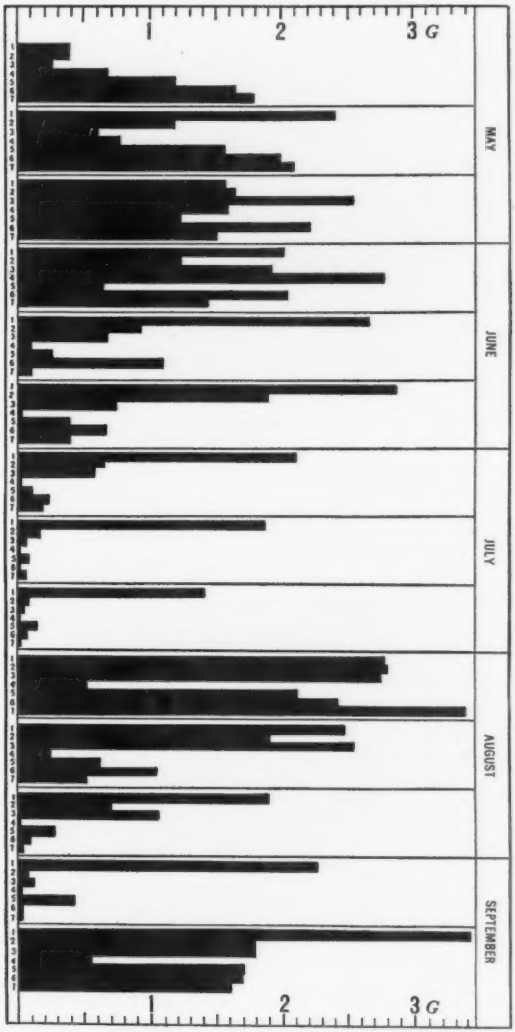

FIG. 2.—Amount of absorption in gm. per two-hour period by Livingston-Koketsu soil points at seven representative stations, during ten-day periods from May 1 to September 20.

The same fluctuation in the water-supplying power of the soil, as shown by the Livingston-Koketsu soil points (fig. 2), is even more marked. Both the individual determinations and their ten-day means show fluctuations closely parallel to those of the growth water percentage data. The close "bunching" of the ten-day means during July and the period ending September 8 is especially suggestive. Since the soil point method was devised in an effort to determine directly the water-supplying power of any kind of soil, independently of its wilting coefficient or any other physical constant, this shows clearly that during such periods of drought all the soils in the locations studied, save one, dropped to a very critical water-delivering power. In the Livingston-Koketsu experiments with wheat and *Coleus* under winter greenhouse conditions, permanent wilting ensued when the water-delivering power of a soil had fallen to a point between 0.04 and 0.11 gm. per two-hour period (as compared with about 15.0 gm. for the same period in a nearly saturated soil). The soil points used in the present determinations, however, have a somewhat greater absorbing power. According to data as yet unpublished, obtained by H. C. DIEHL, the new points have 1.25 times the absorptive power of those used by LIVINGSTON and KOKETSU. The water-delivering power of the soil at the permanent wilting point should therefore be between 0.05 and 0.14 gm. for a two-hour period. This is the case, at least, if we do not take into account the evaporating power of the air at permanent wilting. Since, however, the evaporating power of the air throughout the droughty periods was greater at the stations considered than it was in LIVINGSTON'S greenhouses, we are safe in doing so, and in taking as an approximate water-supplying power at wilting point 0.15 gm. for the two-hour period. It will be seen that during the drought periods all of the stations save one either approached or passed this critical point, and that several of them were well beneath it for a period of thirty days during July and one of twenty during August, with an interval of only ten days between these two prolonged droughts. Further, a comparison with figs. 3 and 5 will show that these were the periods of greatest stress from extremes of temperature and evaporation. It is fairly evident, therefore, that seedlings that are to survive throughout most of the park must be

of species able to get an early start or make sufficiently rapid growth to have well established root systems before the advent of the usual summer droughts.

A more detailed examination of individual stations serves to emphasize the facts already noted in general, and also brings out several edaphic phenomena of considerable interest. It is here that topograph factors appear to function. Thus, station 1 is the least exposed, and also the least well drained, being on the flat floor of a canyon. It is also subject to flooding when there is heavy rain, and the run-off from the tributary gullies comes over the canyon falls. It is not surprising, therefore, to find that it is constantly well above both the wilting coefficient and the Livingston-Koketsu wilting point. It is not surprising, either, to find here the largest number of young seedlings, and a herbaceous vegetation dominated by annuals. On the other hand, the highest upland station, no. 7, is both well drained and quite exposed; in correlation therewith it rapidly loses what water it gains, and persistently holds a place near the bottom of the column during the droughty periods. Few seedlings develop, and the herbaceous vegetation consists largely of grasses and sedges and of perennating prairie plants. The stations on the more or less sloping terrain (no. 6 on the upland and nos. 5, 3, and 2 on talus slopes) present phenomena intermediate between these extremes.

Station 4, on an alluvial flat beside the river, in a maple-elm-ash association, presents an anomalous situation. Starting in the spring with a moderate amount of soil water, it loses rapidly and fails to recover, during the summer rains, to anything like the degree displayed by the other stations. The soil point data confirm its bankruptcy. After it has lost its water during June, it falls to the bottom of the heap during the droughty periods and stays there more persistently than any other station. During the rains, when the others rapidly increased in their water-supplying power, this station rose but little, and then quickly dropped to the bottom again. This behavior may be accounted for in several ways. The soil here is a heavy, silty alluvium, very tenacious of the water it gets. It does not receive the benefit of periodic flooding, as does station 1. The thicket of saplings is so dense that

only the heaviest rains ever penetrate the foliage sufficiently to wet more than the surface of the ground. A large proportion of the soil surface is bare, puddling easily, and thus facilitating direct evaporation. These, and possibly other unnoted factors, can account for the condition here.

EVAPORATING POWER OF AIR (fig. 3).—The effect of the climatic factors that influenced soil moisture conditions is plainly evident in the atmometric data also. There was more rainy and cloudy weather during May than during June, and the rates of evaporation show a corresponding decline during the latter month. Then, with the beginning of the hot, dry weather of July the rates increased suddenly and enormously. There was a sudden drop after the oncoming of the early August rainy period. Throughout August the daily temperatures were markedly lower than those for July (fig. 4), with much cloudy weather, although actual precipitation was confined to brief local showers; with this was correlated a reduction in the transpiration curves to one-half or less of their July heights. A short heated period at the beginning of September brought an increase in the rate, but the ensuing cool, humid days that closed the period of observation brought the curve down, and the season came to an end with a period of very low transpiration rates.

A feature of some interest in the set of atmometric curves is presented by the deep "dip" during the month of June. It was natural that evaporation rates should be higher during July, as already pointed out, but the sharp decrease from the May rates seems at first somewhat anomalous. One possible reason suggests itself in the comparative amounts of general exposure due to the foliation of the trees. The spring of 1921 was late and cool, and during May the trees, especially the oaks, were still nearly naked. As the foliation increased, changes in three of the four main factors controlling evaporation might naturally be expected; direct insolation and air movement would be reduced, and relative humidity probably increased. All of these changes would be in favor of reduced evaporation. The fourth main factor, temperature, increased somewhat during this time. This would have worked in the opposite direction, but presumably the operation of the other three had the greater effect.

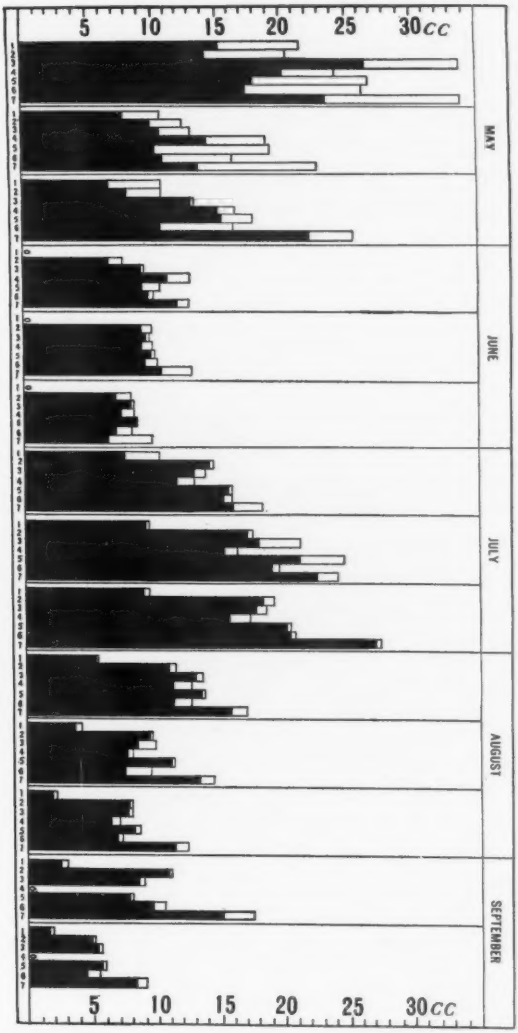

FIG. 3.—Mean daily amounts of evaporation in cubic centimeters from standard spherical black and white atmometers; black columns indicate simple atmometric effect; white extensions, increased evaporation due to direct insolation; a zero at base of column signifies data lacking for the period.

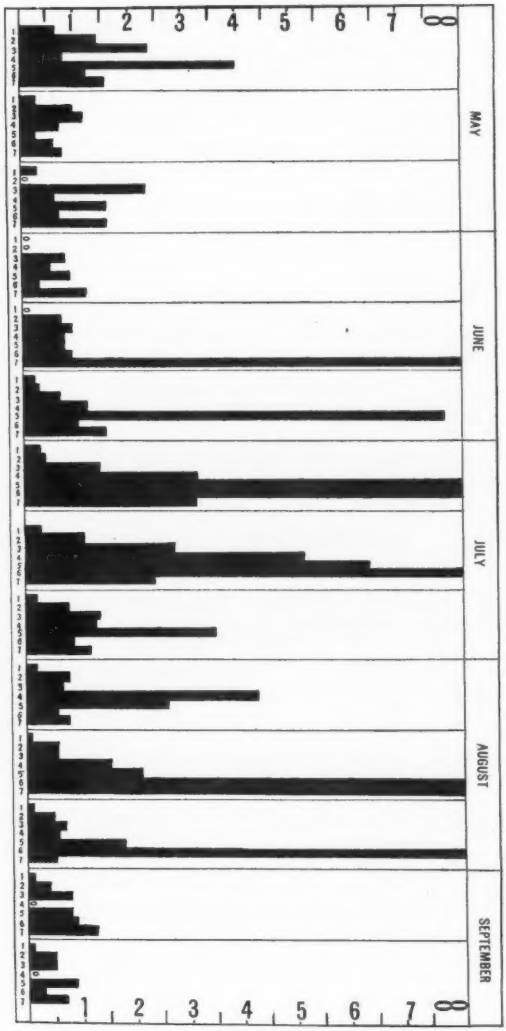

FIG. 4.—Relative xerophytism (ratio of evaporation rate to growth water) at the seven stations; a zero at base of column signifies data lacking for the period.

An examination of the differences between the curves of the separate stations brings to light certain topographical correlations. In the first place, there was a general correlation between the exposure of a station and its evaporation rate. Thus, station 7, the most exposed of the set, shows consistently the highest evaporation rates, while station 1, the least exposed, shows consistently the lowest. Even between these extremes the correlation holds, for of the three talus slope stations, no. 5, the most exposed, shows higher rates than nos. 3 and 2, which were partly sheltered within the canyon.

Again, the more exposed stations showed much more marked variation, both seasonal and diurnal, than did the more sheltered stations. The highest mean daily rate for a ten-day period (26.9 cc. per day, July 21–30) exceeded the lowest mean daily rate (8.1 cc. per day, September 9–20) by 18.8 cc. This may be compared with the excess of the maximum mean daily rate at station 1 (9.2 cc., July 21–30) over the minimum mean daily rate (1.3 cc., September 9–20), which is 7.9 cc. The excess at station 7 is 10.9 cc. greater than the excess at station 1, or a ratio of 2.4. Another notable thing is the relative stability of the daily rates at the more sheltered stations as compared with the greater fluctuation at the more exposed stations. Thus, at the two stations and for the two periods noted, the greatest mean daily rate at station 7 (26.9 cc.) exceeds the greatest mean daily rate at station 1 (9.2 cc.) by 17.7 cc., whereas the least mean daily rate at station 7 (8.1 cc.) exceeds the least mean daily rate at station 1 (1.3 cc.) by only 6.8 cc. The difference during the period of highest evaporation rate is 2.6 times as great as the difference during the period of lowest evaporation rate. The general effect of this factor is strikingly brought out by the "bunching" of the curves during June and September, the low evaporation periods. This greater variability displays itself even more markedly, of course, in the diurnal variations than in the variations of mean daily rates. During the period of high evaporation just cited, for example, the readings at station 7 on three successive days (July 14, 15, and 16) were 31.8 cc., 8.9 cc., and 19.1 cc. respectively, while on the same days readings at station 1 were 9.8 cc.,

3.8 cc., and 10.4 cc. Similarly, even during a period of low evaporation, three successive readings at station 7 give 15.3 cc., 5.5 cc., and 11.6 cc., while at station 1 the corresponding readings are 4.0 cc., 1.4 cc., and 1.8 cc. Examination of the data from stations of intermediate exposure will show correlated results.

The ratios between growth water and evaporation rates, presented in fig. 4, serve to emphasize and render definite the ideas in the foregoing paragraphs. Of course, as FULLER (7) has pointed out, this ratio is a more or less artificial and arbitrary one, yet it is as good a method as we have at present for a quantitative statement of the relative xerophytism of different habitats, and inasmuch as it brings out strongly the cumulative effect of two factors operating in the same direction, it is of value.

The foregoing considerations of the atmometric and soil moisture data suggest strongly the essentially prairie-like summer conditions, even in this woodland island in the prairie, and the intensification of the summer xerophytism of the soil by the summer xerophytism of the air. The greatest evaporating power of the air prevails precisely during those periods when the plants are least able to obtain water from the soil to satisfy it. Summer rains relieve the tension, to be sure, but even after heavy rains the relief is short-lived, and slighter in degree than might be supposed. Only in places at once well endowed with a supply of water and at least fairly well sheltered from extreme transpirational conditions (represented in the present study by station 1) is there any chance for germination and growth of seedlings during the middle of the growing season. This theoretical conclusion is borne out by the existence in such places of annuals as the dominant herbaceous vegetation, and by the presence of large numbers of tree seedlings. Furthermore, it is here also that one finds "superclimax" trees, like *Acer saccharum* and *Asimina triloba*, belonging normally to more mesophytic regions. In the more exposed stations (the extreme being no. 7) the unfavorable summer conditions set in so early and become so severe as to discourage seedling growth. The canyon bottoms therefore receive strangers hospitably and permit of relatively rapid succession, while the exposed uplands conservatively cling to the climax vegetation they have, and permit, in places too xerophytic

even for this, the survival of relict communities, like the conifers on the edges of the cliffs.

INSOLATION EFFECTS.—An examination of the radio-atmometric data serves to emphasize the atmometric phenomena already noted, in addition to its main purpose of getting some idea of the sunlight intensity as this affects evaporation. The evaporation from the black cups of course follows the same general seasonal curve as that from the white, the excess varying according to seasonal and local conditions. The radio-atmometric effect, as one might expect, was greatest during the season of greatest exposure, that is, during the month of May, before the leaves were on the trees. After the first of June the effect was much less marked. Even during the hot weather of July the evaporation rate from the black cups exceeded that from the white by but little.

The general differentiation in the radio-atmometric effect with the development of the foliar screen was accentuated by local variations. Thus, the tendency throughout the season was for a greater difference at station 7, the most exposed of the set, located in an open stand of second growth oak. Station 1, located on a treeless portion of the canyon bottom, in a stand of *Impatiens pallida*, showed a most notable radio-atmometric effect during May, before the surrounding herbage was well grown; after July 1 the effect fell almost to zero, and remained so throughout the rest of the season.

Of course it is not possible to take the radio-atmometric effect as a measure of solar radiation in all its effects on plants. It is intended only as an approximate determination of direct solar radiation on the evaporation of water from a free surface. Taking it as a rough index of the total illumination received, however, we find that during the season when other ecological factors are favorable for the growth of seedlings on the forest floor it is at its maximum, and that it falls off notably after the leafing out of the trees. Presumably then, sunlight conditions conspire with the ecological factors already discussed to make late spring the optimum season for seedling growth, and that at places like station 1, where other conditions are favorable even when they are most unfavorable elsewhere, sunlight intensity falls to an unfavorable level after about July 1, or possibly even earlier. It must be emphasized again,

however, that so little is known about the sunlight relations of plants that attempts at close correlation are for the present unprofitable.

TEMPERATURE (fig. 5).—Temperatures of both air and soil show similar seasonal variations, with high points in July, and a falling off in August and September, interrupted by a brief period of high temperatures during the first few days of the latter month. The figures up to July 1 can be accepted only as approximations, since they are absolute maxima and minima for periods of more than a week, instead of mean daily maxima and minima. For this reason too much significance must not be attached to the greater spread between maxima and minima. Although a greater spread did undoubtedly exist, it probably was not so great as the thermometer readings at the ends of the periods would indicate.

So far as any significance may be attached to the figures before the period of daily readings began, the influence of the diminution of general exposure through the leafing of the trees seems to be at work here also, for during May the maxima both for air and soil show as marked a spread as that shown for the warmer months of July and August. This spread is especially noticeable in the data for soil maxima,[1] inasmuch as it amounts to eight or ten degrees throughout May, falls to a point at one of the June readings, and for the rest of the season never exceeds three degrees. These results agree fairly well with those of MCDOUGALL (14), who found a consistent seasonal variation of about 4° F. between the soil temperatures of typical upland and lowland stations in Illinois forests.

Topographical differences seem to have some influence also, although the correlation is not so clear here as it is in the case of the atmometric and radio-atmometric data. It may be remarked, however, that the high lying stations (typified by no. 7) show the highest maxima both for air and soil, and the low lying stations the lowest maxima. On the other hand, the lowest minima for the air are obtained at the high lying stations and the highest minima at the lower ones. This may be due, among other things, to the denser leaf covering and the greater amount of underbrush at the

[1] Because of the close agreement between the readings for all the stations after July 1, it is not thought worth while to present the soil temperature data in detail.

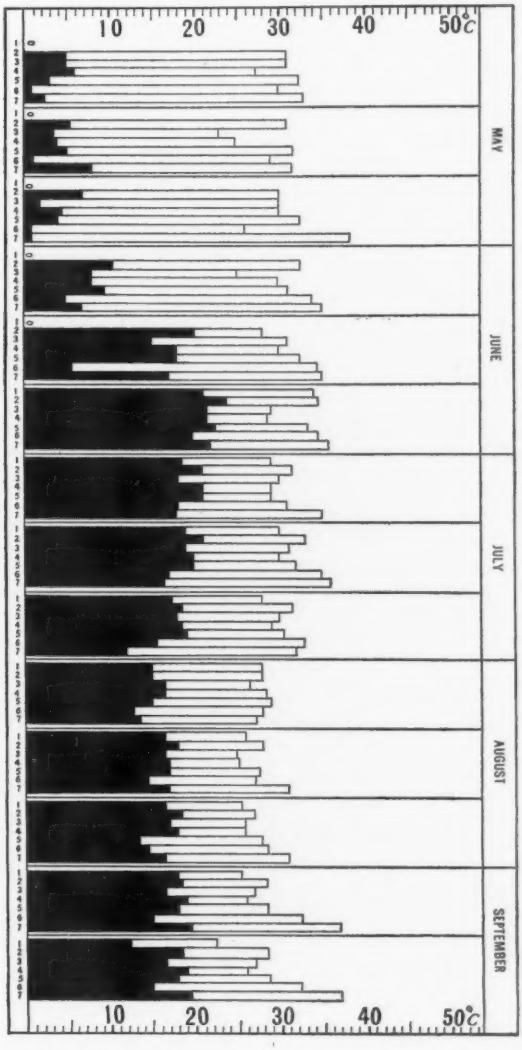

FIG. 5.—Mean daily maximum and minimum air temperatures at the seven stations; a zero at base of column signifies data lacking for the period.

lower stations, holding the lower stratum of air to a certain extent against displacement by air drainage.

One object in obtaining these temperature data was to ascertain whether temperature differences might be correlated with the invasion of lower latitude plants, like *Asimina triloba*, into the lower levels. The data obtained, however, are contradictory. The mean temperatures are undoubtedly higher at the higher lying stations, the last points of invasion, and also the last points of cession by relict northern species. On the other hand, the consistent higher minima at the lower levels might well permit a slightly longer growing period, and perhaps even milder winter conditions. Otherwise stated, the temperature optimum for southern species might not be so nearly approximated on the lower stations as at the higher, but a point above the minimum might be maintained throughout a longer period each year. The main reason for the confinement of southern invaders to the bottom lands, however, must probably be sought in the more favorable moisture conditions at these levels. The writer does not feel that attempts at close correlations between temperature and vegetation over such small differences in altitude would be very profitable at the present stage of development in ecological science. It is interesting to find, however, that fairly consistent small differences in temperature do coexist with small topographical differences.

Summary

1. This paper is a study of the ecological factors at seven representative topographical points in the Illinois State Park at Starved Rock, during the growing season of 1921. The factors studied were (*a*) soil moisture, (*b*) evaporating power of the air, (*c*) evaporating power of solar radiation, and (*d*) temperature of air and soil.

2. Observations were taken with special reference to their influence on seedling growth, because of the importance of the latter as a factor in succession.

3. Soil moisture was found to vary (*a*) seasonally, falling off after the close of the spring rains and reaching a point below the minimum necessary for plant growth during a considerable portion

of the summer, and rising again with the beginning of the fall rains; (*b*) according to the mechanical composition (and therefore retentivity) of the soil; (*c*) to a minor extent according to topography; and (*d*) according to the density of the foliage canopy.

4. The evaporating power of the air was found to vary (*a*) seasonally, increasing until midsummer and falling off afterward; (*b*) according to the state of tree foliation, declining after the forest had become completely clothed; and (*c*) topographically, being greatest for the same period in exposed stations and least in sheltered ones.

5. The evaporating power of solar radiation was found to vary in the same manner as the evaporating power of the air, complementing and emphasizing the data under the latter head.

6. Maximum temperatures were found to vary in much the same manner as the evaporating power of the air. Minimum temperatures of the air were found to be affected by topography in a mode inverse to that of the maxima, being highest at the low lying stations and lowest at the higher lying ones.

7. Certain vegetational phenomena showed a general correlation with the instrumental observations: (*a*) the density of ground cover, number of tree seedlings, and proportion of annuals in the total vegetation of any given association bore an inverse relation to the relative xerophytism; (*b*) in all but one of the stations, conditions were favorable for the development of seedlings only in spring and fall; (*c*) in the climax forest for the region (upland oak woods) the water-supplying power of the soil consistently fell nearly or quite to zero during the summer drought period; (*d*) the location of "subclimax" and "superclimax" associations showed closer correlation with water relations than with temperature.

The writer owes a debt of special gratitude to Professors H. C. COWLES and G. D. FULLER of the University of Chicago for their encouragement and assistance in the preparation of the data here presented. The courtesy of the Illinois State Park Commission should also be acknowledged.

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NOTES ON NEOTROPICAL ANT-PLANTS

I. CECROPIA ANGULATA, SP. NOV.

I. W. BAILEY

(WITH PLATE XV AND EIGHT FIGURES)

Introduction

In a previous paper (1) the writer discussed the significance of the anatomical peculiarities of a number of Ethiopian ant-plants. So many features of unusual interest were encountered in studying these plants, that it seemed desirable to extend the scope of the investigation, and to include certain neotropical myrmecophytes for comparative purposes. With this end in view, the writer spent the summer of 1920 at William Beebe's Tropical Research Station in British Guiana, where the following ant-plants (*Tococa aristata* Benth., *Triplaris surinamensis* Cham., *Tachigalia paniculata* Aubl., *Cordia nodosa* Lam., and *Cecropia angulata*, sp. nov.) grow in close proximity to the laboratory.

Since the publication of SCHIMPER'S (8) much quoted investigations, *Cecropia adenopus* Mart. has been considered one of the most classical illustrations of myrmecophytism. SCHIMPER interpreted the "Müllerian food bodies" and the "prostomata" of this ant-plant as adaptations for enlisting the services of an aggressive army of Aztecas, which protect their host against the attacks of the destructive, leaf cutting, Attine ants; a conclusion that has been assailed by VON IHERING (4), ULE (9), RETTIG (7), FIEBRIG (3), and other critics of the BELT-DELPINO theory of myrmecophily. In view of the important rôle that has been assigned to *C. adenopus*, in discussions concerning the significance of ant-plant symbioses, the writer welcomed the opportunity of studying a somewhat similar species of this interesting genus. The results of the investigation are summarized in the following pages.

Taxonomy

One of the first difficulties encounted in studying a neotropical biocœnose, in which representatives of the higher plants, ants,

coccids, and other insects are closely associated, is the identification of the organisms concerned in the complex. Of course, the principle of significant figures must be considered in biology, as in physics and mathematics. The most detailed field observations and carefully planned experiments may lose much of their significance if an investigator fails to secure adequate information concerning the identity of the plants and animals with which he is working. In most cases, therefore, it is advisable to prepare museum specimens which may be preserved as a record for verification by other investigators. Typical herbarium specimens of all of the plants to be discussed in this and in subsequent papers have been deposited in the Gray Herbarium of Harvard University. Specimens of the insects have been preserved in the collections of Professor W. M. WHEELER, who collaborated with the writer in the investigation of the myrmecophytes of the Kartabo region. The ants were identified by him, the coccids by Mr. HAROLD MORRISON of the United States Bureau of Entomology, and certain parasitic Hymenoptera by Professor C. T. BRUES.

In dealing with *Cecropia*, one is concerned with a group of plants which present many taxonomic difficulties. The leaves of mature plants frequently are much too large for herbarium sheets of standard dimensions, and the inflorescences are difficult to season for museum purposes. Thus many of the descriptions of species are based upon the study of more or less fragmentary material. Furthermore, there appears to be as yet no consensus of opinion as to which of the foliar and floral characters are of the greatest diagnostic value. In view of these facts, the writer devoted considerable attention to the investigation of the variability of the morphological characters of the Kartabo species of *Cecropia*.

There proved to be two distinct species, a myrmecophytic species, with a well developed trichilium and numerous food bodies, and a non-myrmecophytic species, which is entirely devoid of these structures. The latter is considered by Dr. E. H. SNETHLAGE to be a variety (*decurrens*) of *C. sciadophylla* Mart. The former does not agree with any previously described species, and owing to its association with ants, was studied more intensively.

During the earlier juvenile stages the leaves of this species are small, ± 6 cm. long, ± 2 cm. wide, simple, lanceolate, finely serrate, pilose above and densely albido-tomentose below. The subsequently formed leaves increase rapidly in size, forming first three, then five, and ultimately nine to eleven lobes (text figs. 1, 2). As the juvenile leaves develop lobes, they lose their marginal serra-

FIG. 1.—*Cecropia angulata:* leaves from juvenile plants of different ages, showing white tomentum and formation of lobed lamina; ×⅛.

tions and become sharply asperate upon the upper surface. The transitions from the juvenile to the typical adult foliage are gradual, and may be deferred until relatively late stages in the ontogeny of the plant. Thus the large deeply lobed leaves of tall saplings may retain many of the juvenile characters, that is, asperate upper surface, chartaceous texture, conspicuous white tomentum on the under surface, acuminate lobes, etc. The leaves of adult indi-

viduals are huge, 56–98 cm. long, 56–84 cm. wide, coriaceous, glossy glabrous above, and are provided with only a microscopic layer of closely appressed white hairs in the areoles of the lower

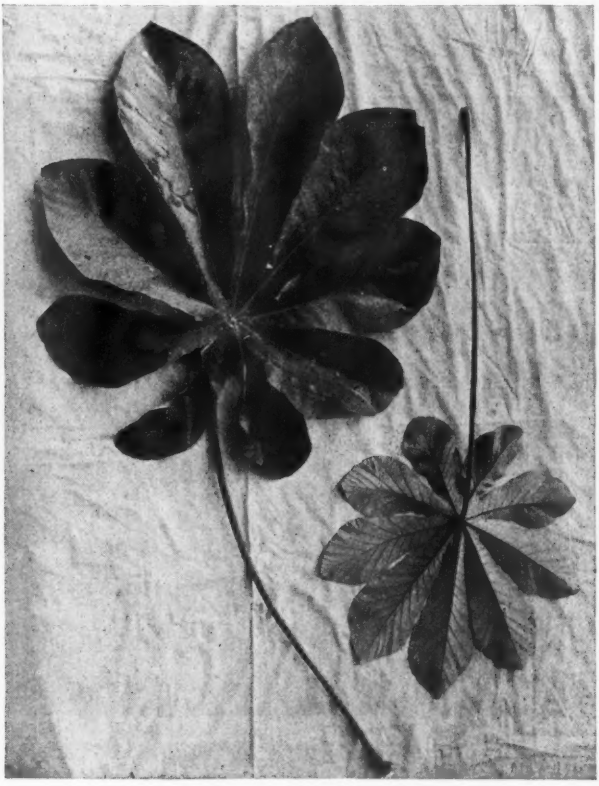

FIG. 2.—*Cecropia angulata:* typical leaves from tall tree, showing variability in size; $\times \frac{1}{14}$.—Photograph by JOHN TEE-VAN.

surface. They are divided to within 4–7 cm. of the base into 9–11 cuneate-obovate or spatulate lobes which have undulate margins (text fig. 2).

Although at first sight most of the vegetative characters appear to be extremely variable, many of them are relatively stable during

specific stages in the ontogeny of the plant. For example, the leaves of adult individuals always are deeply lobed and undulate on the margins, never scabrous on the upper surface or conspicuously

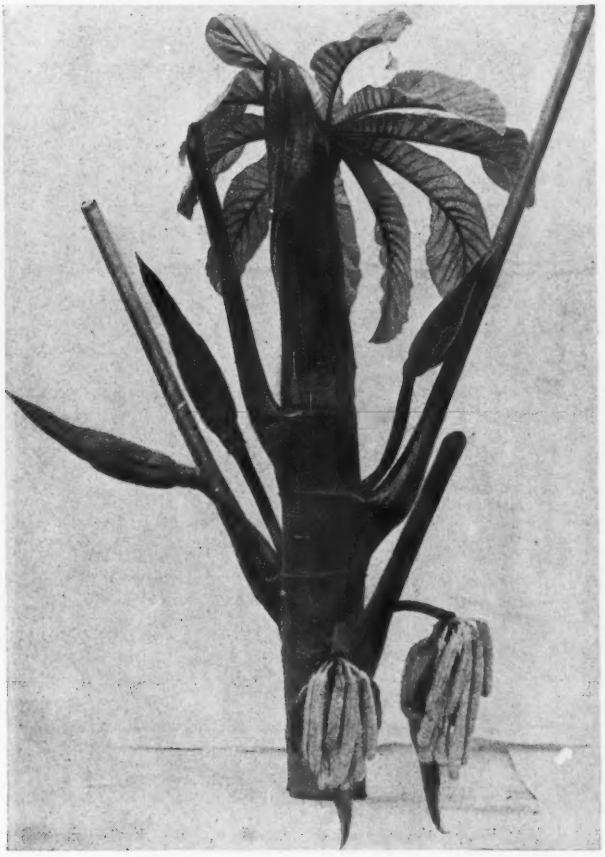

Fig. 3.—*Cecropia angulata:* terminal shoot of tall, vigorous young tree, showing ♂ inflorescences, and foliar and florial bracts; $\times\frac{1}{10}$.—Photograph by JOHN TEE-VAN.

tomentose below; whereas the leaves of juvenile plants always are hairy or sharply asperate above, and are densely albido-tomentose on the under surface. It is evident, therefore, that in distinguish-

ing species of *Cecropia* it is essential to compare leaves from plants of similar age classes, and, so far as possible, to avoid generalizations based upon highly variable, transitional types of foliage, such as occur on saplings.

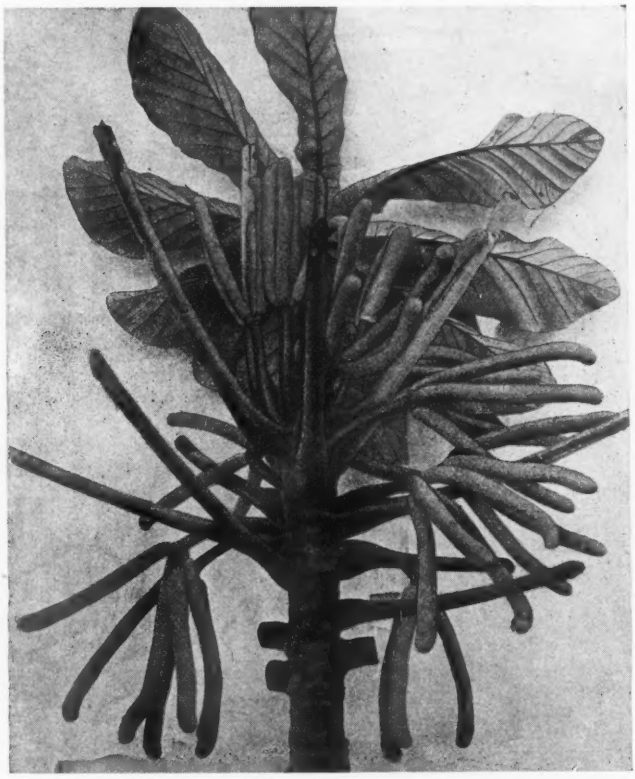

FIG. 4.—*Cecropia angulata:* terminal shoot of old, slow growing tree, showing ♀ aments in different stages of development; $\times\frac{3}{13}$.—Photograph by JOHN TEE-VAN.

Certain of the floral characters are variable, whereas others are relatively stable. The bracts which envelop the young inflorescences are coated during the later stages of their development with dense, rufous tomentum, and are frosted with long white hairs. The male and female aments (text figs. 3, 4) vary in size

during different stages of their ontogeny, but the former (text fig. 5*A*) retain their juvenile angularity, whereas the latter (text fig. 6*D*) become nearly cylindrical at maturity. The peduncles vary considerably in length, but are asperate in both sexes. The female inflorescences are characterized by having one or more perigones in the sutures between the short, stout, conferruminate

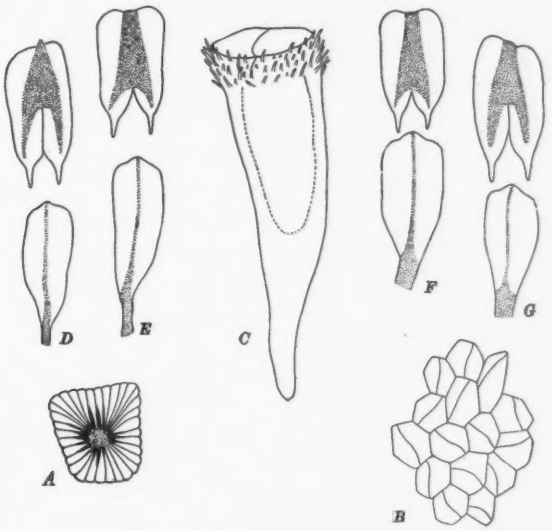

FIG. 5.—*Cecropia angulata: A*, cross section of ♂ ament, ×2.5; *B*, surface view of portion of ♂ ament, showing pentangular and hexangular, apically cleft perigones, ×10; *C*, ♂ perigone, showing collar of short, stiff hairs, and position of perigonial chamber, ×22; *D*, lower stamen of pair; *E*, upper stamen of same pair; *F*, upper stamen of pair from another perigone; *G*, lower stamen of this pair; (*D–G*) ×22.

pedicels (text fig. 7*C*). The clavate, pentangular or hexangular, apically cleft male flowers are not jacketed by a dense mat of long, interlacing trichomes, but are provided with a collar of short, stiff hairs (text fig. 5). The perigonial chamber is confined to the upper half of the flower, and the caudate anthers are borne on short filaments which become extraordinarily broad and membranaceous at the time of dehiscence (text fig. 5). The filaments, connectives, and anthers vary considerably in size and shape (text fig. 5*D–G*);

for example, the upper anther of each pair tends to be somewhat smaller, and to be attached nearer its base to a longer filament. The connective may or may not project beyond the apex of the anther. The pentangular or hexangular perigones of the female aments (text fig. 6) are characterized by having three distinct types of trichomes. They are jacketed both internally and externally by dense mats of long, interlacing hairs (text fig. 7). In addi-

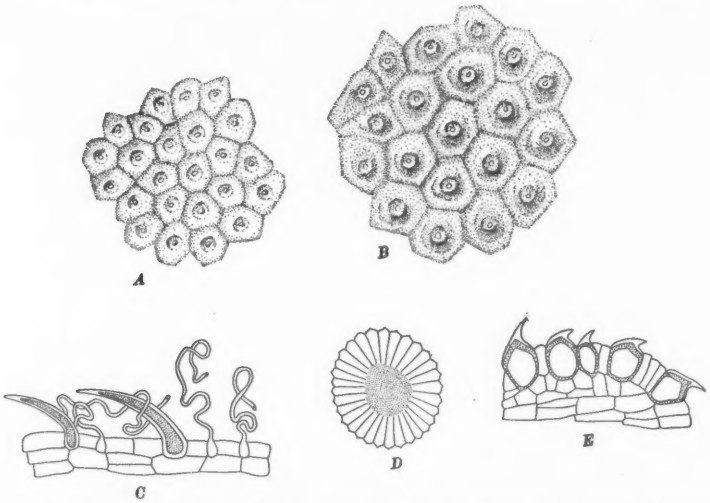

FIG. 6.—*Cecropia angulata:* *A*, surface view of portion of ♀ ament, showing pentangular and hexangular perigones at fertilization, ×10; *B*, surface view of portion of ♀ ament, showing enlargement of perigones during earlier stages in formation of seed, ×10; *C*, two types of trichomes from inner wall of perigone, ×315; *D*, cross-section of ♀ ament at fertilization, ×2.5; *E*, trichomes from outer apical portion of perigone (similar bristles occur on style); ×315.

tion, they have a crown of extremely short, stout bristles on the margins of their exposed apical surface, and a fringe of longer bristles which project into the constricted upper portion of the perigonial chamber (text fig. 6). The glabrous, almond-shaped ovary is mottled, dark gray, and bears a cylindrical style which terminates in a comose stigma (text fig. 7). The style is provided with short, stout bristles, such as occur on the apical portion of the perigone. During the development of the seed, the perigone

enlarges and becomes somewhat modified in form and structure (text figs. 6, 7). The white tomentum is carried outward, so that the lower two-thirds of the flowers are not held together by inter-

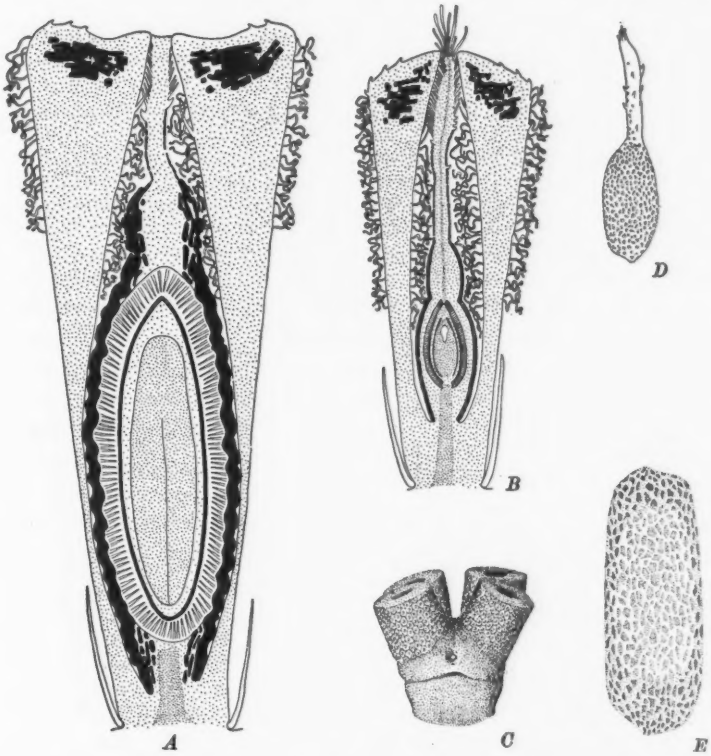

FIG. 7.—*Cecropia angulata:* *A*, longitudinal section of ♀ perigone and nearly mature seed, showing embryo and various seed coats, ×31; *B*, longitudinal section of ♀ perigone, style, ovary, and ovule, showing various types of trichomes, ×31; *C*, basal portion of ♀ inflorescence, showing perigone at point of contact of conferruminate pedicels, ×4; *D*, ovary and style, ×18; *E*, mature seed, ×20.

lacing hairs, and an annular depression is formed in the exposed outer surface of each perigone. At maturity the scurfy, dark reddish brown, oblong seeds (text fig. 7*E*) have a more or less symmetrical, lozenge-shaped, triangular or rectangular contour in cross-section.

Owing to the variability of many of the floral characters during the enlargement of the aments, there is a considerable element of uncertainty in comparing inflorescences which are not in equivalent stages of differentiation. In the case of the male aments, the anthers, and especially the filaments, do not attain their most characteristic size and shape until just before dehiscence. Furthermore, there are two distinct stages in the differentiation of the female aments, one before and one after fertilization. The changes in the size and form of the perigones during the maturation of the ovules, and subsequently during the enlargement of the seeds, are reflected in the aments, whose external characters become correspondingly modified. The significance of these developmental stages does not appear to have been appreciated fully by a number of students of the species of *Cecropia*. The aments, perigones, stamens, seeds, etc. are described and are used for diagnostic purposes without reference to their variability or to their particular stage of development. Until more is known concerning the variability of the various species of *Cecropia*, and until their more stable diagnostic characters have been isolated and fully described, it is desirable to give rather comprehensive descriptions of new species. The following description of the myrmecophytic species of the Kartabo region is based upon the study of typical adult specimens. The juvenile characters have been referred to previously.

Cecropia angulata, sp. nov.—Arbor 10–25 m. altus, caulibus ramisque juvenibus argute asperatis formicosis (*Azteca*). Folia ampla rubella vel viridia 56–98 cm. longa 56–84 cm. lata profunde 9–11-lobata, lobis cuneato-obovatis vel spatulatis, apice obtusis vel rotundatis saepissime mucrontis, margine undulatis, lobo medio 36–60 cm. longo 13–24 cm. lato, nervis secundariis 15–20, lamina supra glabra nitente (post exsiccationem castanea obscurata) infra in nervis venis venulisque galbrata, in areolis solis tenuiter (microscopice) albido araneoso-tomentosa et in disco centrali breviter griseo-villosa, petiolo cylindrico (post exsiccationem costato) 50–120 cm. longo glabro vel albido-tomentoso ad basin incrassato et cum trichilio albido (tardius castaneo) instructo. Stipulae vaginantes maximae castaneae paullo griseo-tomentosae. Amentae ♂ 14–18 rectae rigidae *angulatae* 5–12 cm. longae 4–7 mm. crassae in

pedicellis tenuibus 5–17 mm. longis gestae et in spatha castanea griseo-tomentella fusiformi ad basin constricta 14–16 cm. longa inclusae. Amentae ♀ 4 rectae rigidae vel apice paullo curvatae cylindricae ante anthesin 9–12 cm. longae 7–8 mm. crassae (tardius 13–17 cm. longae 11–13 mm. diametro) in pedicellis crassis conferruminatis 3–7 mm. longis gestae et in spatha castanea griseo-tomentella quadrangulata obtusa 10–12 cm. longa inclusae. Pedunculi argute asperati compresso-cylindrici, ♂ 9–12 cm. longi 8–11 mm. crassi, ♀ 8–10 cm. longi 7–10 mm. crassi. Perigonia ♂ clavata pentangularia vel hexangularia 2–3 mm. longa, filamentis in maturitate membranaceis 0.5–1.4 mm. longis 0.3–0.5 mm. latis, antheris caudatis 0.8–1.0 mm. longis 0.4–0.5 mm. latis. Perigonia ♀ pentangularia vel hexangularia cum albido tomento vestita ad anthesin 1.5–2.0 mm. longa deinde usque ad 3.0–3.5 mm. elongata. Stylus cylindricus ovarium aequans vel eo longior. Stigmata comosa. Fructus maturus furfurosus rubidus 2.0–2.5 mm. longus.

Kartabo region, British Guiana: *I. W. Bailey* (1920), nos. 3, 4, 5, 6, 8, 9, 14, 15, and 17; Kangaruma, British Guiana: *H. A. Gleason* (1921), no. 198.

The fistulose stems of *Cecropia angulata* are inhabited by four distinct species of *Azteca;* a majority of the plants are colonized by a black species, *A. constructor* Emery, a considerable number by a yellowish species, *A. alfaroi* Emery, and an occasional isolated individual by either *A. instabilis* F. Smith or *A. trigona* subsp. *mediops* Forel. The following observations upon the habits of the guest ants are based upon a study of the first two species.

Of the coccids which are associated with *Azteca*, *Pseudococcus rotundus* Morrison is the commonest species. *Akermes quinquepori* Newstead and *Pseudococcus bromeliae* Bouché are of more or less sporadic occurrence.

Are Cecropias protected by their guest ants?

In studying the remarkable leaf cutting and fungus growing habits of the neotropical Attine ants, BELT (2) became much impressed by the efficiency of these insects in defoliating large numbers of native and introduced plants, and he was led to wonder how tropical vegetation has survived their devastating attacks. He inferred that the leaves of many plants are distasteful to the

ants or are unsuitable for their purposes, and that other plants are provided with special means of defense. He concluded that the so-called bull's-horn Acacias and other myrmecophytes are protected by their guest ants, which drive away their leaf cutting relatives. MÜLLER (6) and SCHIMPER (8) endeavored to prove that the myrmecophytic species of *Cecropia* are protected by the ants which inhabit their fistulose stems and branches. They found that plants which were colonized by Aztecas were not molested by Attine ants, whereas uninhabited individuals were more or less completely defoliated by them.

That BELT, MÜLLER, and SCHIMPER tend, on the one hand, to exaggerate the destructiveness of the leaf cutting ants, and on the other hand to overemphasize the protection afforded by the guest ants, has been suggested by VON IHERING (4), RETTIG (7), ULE (9), FIEBRIG (3), WHEELER (10), and other critics of the theory of myrmecophily. Several of these investigators call attention to the fact, previously noted by MÖLLER (5), that the leaf cutting ants feed upon a great variety of plants, and show no particular preference for the foliage of *Cecropia*. Thus, although the Attine ants frequently are troublesome pests in gardens and orchards, their feeding habits under normal conditions are such that they are not likely to exterminate indigenous species. According to VON IHERING'S computations, 183 nests of leaf cutting ants consume no more foliage during a year than does a single cow. In many cases the myrmecophytes grow in regions, such as swamps and periodically inundated areas, where the fungus growing Attas do not occur. Furthermore, during the earlier stages of its development *Cecropia* is not inhabited or protected by its putative guardians. In addition, it has been shown that plants which are not inhabited by Aztecas may remain unmolested by Attas for long periods, and that trees which are inhabited may be seriously injured by phytophagous insects and sloths. Of course it must be admitted in this connection that the discrepancies between the conclusions of MÜLLER and SCHIMPER and those of ULE, VON IHERING, and others, may be due to the fact that they were concerned with different species of Attine ants. Furthermore, it may be argued that the juvenile

plants do not need the protection of the Aztecas, since they are immunized by various protective devices.

In the forests of the Kartabo region there are numerous colonies of the common leaf cutting and fungus growing ant, *Atta cephalotes* L. The writer found, as MÖLLER had previously done in the case of *A. discigera* Mayr., *A. hystrix* Latr., and *A. coronata* Fabr., that this ant utilizes the leaves of a great variety of plants in the construction of its fungus gardens. In virgin and second growth forests, it seldom works for any considerable length of time upon a particular type of plant, but continually shifts its activities from one species to another. Owing to this fact and to the rapid recovery from injury by plants in moist tropical environments, the effects of its attacks upon a given species appear to be more or less evanescent. Its normal leaf cutting habits, however, may be considerably modified under unusual or abnormal conditions. It frequently exhibits a strong preference for plants to which it has not previously been accustomed. Thus its attacks upon certain exotic plants in gardens and orchards at times may prove to be singularly persistent and destructive.

In many cases *Cecropia angulata* is not colonized by its guest ants until it has attained a considerable size. This is largely due to the fact that the young, fecundated queens, which initiate the new colonies, are killed by a Hymenopterous parasite, *Conoaxima aztecicida* Brues. Such plants are no more subject to defoliation than are the inhabited individuals. In order to determine whether the leaves of the juvenile *Cecropia* are distasteful to the leaf cutting ants, or are unsuitable for their purposes, a number of young plants were placed in close proximity to a large nest of *Atta cephalotes*. Leaves of adult Cecropias and of various other plants were used as controls. Although the ants worked upon this material in a more or less sporadic fashion, and showed a strong preference for certain types of leaves, they devoted no more attention to the mature than to the juvenile foliage of *Cecropia angulata*. In view of the fact that both BELT and SCHIMPER admit having seen young myrmecophytes defoliated by Attas, there appears to be little evidence in favor of the suggestion that juvenile ant-plants are less suscept-

ible to the attacks of phytophagous insects than are the adult individuals.

In defending the theory of myrmecophily, SCHIMPER placed great emphasis upon the discovery, in the Corcovado near Rio de Janeiro, of a species of *Cecropia* which is devoid not only of ants, but also of prostomata and Müllerian food bodies. He inferred that this *Cecropia* possesses no adaptations for attracting a defending army of Aztecas, because it is protected by a waxy coating which prevents the leaf cutting ants from climbing its stems. *Cecropia sciadophylla* Mart. var. *decurrens* Snethlage is not colonized by Aztecas, but, as will be shown later, is provided with conspicuous and highly differentiated prostomata. The external surfaces of the plant are scabrous and afford a firm foothold for ants, as evidenced by the fact that several species of these insects were seen climbing its stems and branches. This species of *Cecropia* is no more subject to defoliation by Attas than is *Cecropia angulata*. That the leaves may be utilized in the construction of fungus gardens is shown by the fact that, when cuttings from plants of various ages are placed near nests of *Atta cephalotes*, the ants frequently transport a portion of the foliage into their subterranean dwellings.

SCHIMPER'S critics place considerable emphasis upon the fact that the myrmecophytic Cecropias may be inhabited simultaneously by two or more distinct genera of ants. To infer from this, however, that the Aztecas are indifferent to the presence of other ants is somewhat misleading. Although species of *Cecropia* were found that were inhabited by *Cryptocerus*, *Crematogaster*, stingless bees, etc., these insects were always confined to the older and lower internodes, which had been abandoned by the Aztecas. In spite of this marked segregation of the colonies in different levels of the stem, fierce conflicts may be waged for possession of the intervening internodes. Thus, the internodal cavities, where the colonies come in contact, frequently are filled with the corpses of dead warriors. The Aztecas are dominant, and in general do not tolerate the presence of other ants, in those portions of the stems and branches which are provided with leaves and food bodies. SCHIMPER found that when leaf cutting ants were deposited upon the terminal portions of a *Cecropia*, they were quickly seized by the Aztecas, if

their presence was discovered, and were hurled to the ground. How then may one account for the defoliation of trees which are inhabited by Aztecas? When a *Cecropia* is touched or shaken, the angry and aggressive Aztecas rush out of their nests and swarm over the whole plant, but under normal conditions only a limited number of workers are visible on the stems and bases of the petioles. Furthermore, there are periods during which the entire colony is quiescent, that is, has withdrawn into its nest. It is well known that these periods of quiescence are not the same in the case of different species of ants. Thus, certain ants are nocturnal, others are active at temperatures when other species are inactive, etc. In other words, as suggested by MÜLLER and MÖLLER, a *Cecropia* may be defoliated by leaf cutting ants during periods when the Aztecas are quiescent.

Prostomata

Above the insertion of every leaf in *Cecropia adenopus* there is a shallow groove, which terminates just below the next node in a roundish depression (text fig. 8). As the external depression corresponds to an internal one, the wall of the fistulose stem is very thin at this place, and is a mere diaphragm in a tube. SCHIMPER showed that this diaphragm is devoid of hard and tough elements (fibrovascular bundles, collenchyma, lignified parenchyma, etc.), such as occur in the adjoining portions of the stem. He inferred from this that the diaphragm originated as an adaptation for facilitating the entrance of ants. At the phylogenetic commencement of symbiosis, the ants bored an entrance through the groove, evidently because the wall of the stem was somewhat thinner there. In accordance with a custom that is almost invariably followed and is connected with the domestic arrangements in their nests, they tended to penetrate into the internodal cavity at its upper extremity (at the apex of the groove). All features which facilitated their entrance at this place were retained in the struggle for existence, and were accentuated through natural selection. This led eventually to the differentiation of a thin, weak diaphragm or prostoma (VON IHERING). In other words, although SCHIMPER admitted that the groove is due to the pressure of the axillary

bud, he maintained that its terminal portion is a highly specialized adaptation, acquired through the action of natural selection. On the contrary, RETTIG and FIEBRIG assert that the prostoma is merely the youngest or less highly differentiated portion of the groove, and that it is produced by the pressure of the axillary bud and other growth phenomena in the elongating internodes. The former investigator is of the opinion that the ants are deterred from excavating in the lower portion of the groove, not by mechanical obstructions, but by the occurrence of "laticiferous vessels" which are absent in the prostoma. It is to be emphasized in this connection, however, that RETTIG'S and FIEBRIG'S statements do not necessarily invalidate SCHIMPER'S conclusion that the diaphragm is an adaptation which originated as a modification of a previously existing structure.

Under most growth conditions *Cecropia angulata* does not form a shallow groove which terminates in a conspicuous circular pit (text fig. 8). The more or less fusiform depression or rill is somewhat deeper in the upper than in the lower portions of the internode, but the differentiation of specialized or mechanical types of tissue is retarded throughout its extension (fig. 1). As the walls of the internode increase in thickness, after the initiation of secondary growth, this fusiform diaphragm of delicate parenchyma is slowly reenforced by tougher and denser tissues (fig. 3). The metamorphosis begins at the base of the groove, and gradually extends upward, but the ants excavate their exits before these changes have progressed very far. It is evident, therefore, that in the case of the myrmecophytic *C. angulata*, the whole groove is a potential prostoma. The exact location of the aperture is determined, not by the presence or absence of resistant tissues or of "latex" vessels, but by the relative thickness of different portions of the diaphragm. That the whole groove is a potential prostoma, and that the ants merely excavate their exits and entrances in its thinnest and most easily perforable portion, are indicated by the behavior of young queens in juvenile plants. In many instances, several queens attempt to occupy the same internode, and as many as five entrances were found cut at different levels of a single groove. Not only do the queens cut through the basal portions of the diaphragms under such conditions, but they may even excavate

entrances in portions of the internodes which are not provided with preformed depressions.

It may be argued that in *C. angulata* the whole groove has been modified as an adaptation to ants. Such an assumption is not warranted, however, when important facts in the anatomy of the non-myrmecophytic *C. sciadophylla* var. *decurrens* are taken into consideration. Although this species is not inhabited by Aztecas, it is provided with more tenuous and highly specialized diaphragms than is *C. angulata* (text fig. 8; fig. 2). The internodal groove is very

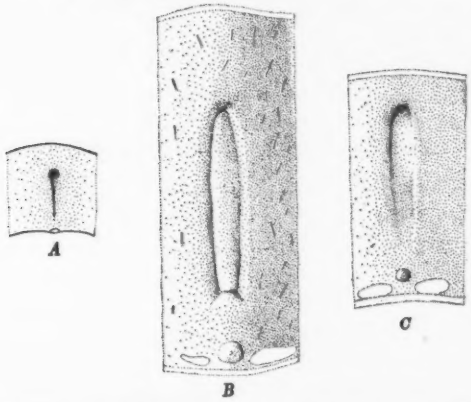

FIG. 8.—Prostomata or internodal diaphragms of various species of *Cecropia*: *A*, *C. adenopus*, after SCHIMPER; *B*, *C. sciadophylla* var. *decurrens*; *C*, *C. angulata*; ×½.

broad and deep, and the diaphragm, which is entirely devoid of tough tissues and secretory vessels, is composed of extremely thin layers of delicate parenchyma. Such facts as these suggest that the so-called prostoma of *C. adenopus*, and of other myrmecophytic species of *Cecropia*, is not an adaptation for attracting ants, but is merely a structural peculiarity, produced by the pressure of the axillary bud, which is utilized by the ants in their parasitism upon the plants.

Feeding habits of guest ants

The *Azteca* colonies are initiated by young fecundated queens which cut entrances into the fistulose stems of juvenile plants. Although I examined hundreds of plantlets of *C. angulata*, none

of any considerable size were found that had been entered by but a single queen. The queens are so numerous that many of the successive internodes become inhabited, and, as already stated, one not infrequently finds that several queens have penetrated into the same internodal cavity. So far as it was possible to determine, however, a large proportion of these queens perish before they have produced a brood. A very considerable number are killed by the parasitic *Conoaxima aztecicida*, others are killed by their rivals in conflicts for possession of a given internode, and, as soon as the workers become numerous, they cut through the nodal partitions and kill all but one of the surviving queens.

When a young *Azteca* queen enters an internodal chamber, she covers the entrance aperture with a layer of triturated pith. The entrance subsequently becomes occluded by callus, which continues to grow internally, and finally projects some distance into the medullary cavity (fig. 4). Thus the queen is sealed within the internode during the period when she is initiating the new colony. In view of the fact that the queen is unable to leave her nest in search of food during a period of two months or more, MÜLLER, VON IHERING, and FIEBRIG infer that she must feed upon medullary tissue and the inwardly projecting callus or "stomatome." It should be noted in this connection, however, that such an assumption is based upon two more or less fallacious premises: (1) that the queen must feed during her period of isolation, and (2) that tissues which are gnawed or excavated by ants actually are eaten by them. Most students of the Formicidae are familiar with the fact that female ants are able to do without food, except such as is stored in their own bodies, for the greater part of a year, while they are founding their colonies. Furthermore, it is well known that many ants tend to gnaw into and smooth the walls of their nests, regardless of whether they are composed of living tissues or of inert materials. I was unable to find any evidence that the *Azteca* queens feed upon the tissues in the young internodes of *C. angulata*. The so-called stomatomes, upon which MÜLLER and VON IHERING place so much emphasis, are not uncovered and cut back by the queens until just before the first workers are ready to emerge from the nest, nor do they excavate the medullary tissue to any consider-

able extent, except when in search of material with which to block up the newly formed entrance aperture. Although VON IHERING is of the opinion that the luxuriant growth of callus is due to the stimulus of some substance excreted by the queens, I found that homologous structures may be produced by purely mechanical injuries.

With the advent of the first workers, the entrance to the primordial chamber is reopened, and the young colony either migrates to a higher internode or cuts through the nodal partitions into adjoining cavities. VON IHERING states that the Aztecas always abandon the primordial chamber and never perforate its upper and lower walls. Such is not invariably the case in *C. angulata*, for primordial chambers were frequently found in direct communication with internodes which were not provided with prostomal openings. Regardless of its exact mode of origin, the permanent domatium soon becomes stocked with food bodies by the young workers. These small beadlike structures (fig. 6), which are packed with fat and protein, are formed in large numbers in a curious cushion or mat of hairs, situated at the base of each petiole. The ripe food bodies are so assiduously collected by the ants that it is almost impossible to find one *in situ*, except in young uninhabited plants. Indeed, the ants frequently trim away the surrounding hairs and dig out the immature food bodies. SCHIMPER interpreted these so-called Müllerian corpuscles, and similar structures which occur on the leaflets of certain myrmecophytic species of *Acacia*, as metamorphosed glands or highly specialized allurements for attracting ants. RETTIG and others, however, have called attention to the fact that such glands occur on plants that are not frequented by ants, and it is difficult for the adherents of myrmecophily to account for such occurrences without resorting to the purely gratuitous assumption that they are survivals from former symbioses. ULE is of the opinion, in addition, that the expenditure of carbohydrates and nitrogenous substances, contained in these corpuscles, is not compensated for by the protection which the ants afford to the plants.

Although most investigators agree that the food bodies are an important item of food in the diet of the Aztecas, it has been

suggested that there are other potential sources of food in *Cecropia*. Thus, VON IHERING and FIEBRIG maintain that the imagines feed upon the succulent medullary tissues in immature internodes. It is true that the ants cut away the softer portions of the pith down to a hard, smooth peripheral layer of medullary tissue, but I found no evidence to indicate that this is not purely a process of house cleaning, such as occurs in many ant nests. In the moist, warm interiors of plants, ants have to contend with luxuriant growths of fungi which obstruct the cavities and interfere with the brood, unless they are held in check. The ants trim away the hyphae and cut back the substratum upon which these organisms tend to grow. FIEBRIG records having seen Aztecas busily engaged in excavating the pith, and in casting fragments of medullary tissue from their entrances, but such observations cannot be interpreted as evidence that the ants actually feed upon the tissues that they are removing.

Most students of the myrmecophytic species of *Cecropia* have found coccids associated with the ants which inhabit the fistulose stems. Their presence has been variously interpreted. BELT, MÜLLER, and ULE consider that they are tended by the ants which feed on their sugary exudations, but FIEBRIG states that the insects "in keinen direkten Verhältnis zu diesen Ameisen stehen." Having found a very close and significant relation between ants and coccids in most Ethiopian ant-plants, I devoted particular attention to the investigation of their behavior in *C. angulata*. I did not succeed in finding a single large, ant-inhabited specimen which did not contain numerous coccids. When a tree is split open the ants are as solicitous for the welfare of the coccids as they are for that of their eggs, larvae, and pupae. They seize them in their mandibles and carry them about until some unopened portion of the plant is found where they may be deposited in safety. In artificial nests, the workers spend hours in tending and stroking the coccids, and in feeding upon their sugary exudates. In view of these facts, it cannot be doubted that the miniature milch cows are an important source of liquid carbohydrates for the ants.

As in many of the African myrmecophytes, the ants excavate pits in the walls of their domatia which enable the coccids to reach

and feed upon the softer tissues of the *Cecropia*. Such excavations are essential, owing to the fact that the internodal, medullary cavity is entirely jacketed by a dense, horny layer of sclerenchyma. In the African ant-plants, the ants cut through to the cambium and induce the formation of a nutritive callus. In *C. angulata* the pits are not located in the sides of the internodal chamber, but in the nodal diaphragms. At the time when the ants begin their excavations, the nodal partition consists of five distinct layers (figs. 5, 7). The soft, internal layer, which is provided with strands of conducting tissue and which is fed upon by the coccids, is separated from the external layers of porous, medullary tissue by two layers of dense, thick walled tissue. The ants remove the two external layers and cut circular pits in the underlying sheets of horny sclerenchyma (figs. 8, 9). The coccids sit in these pits and thrust their setae into the succulent tissue which is thus exposed. That the pits are not made by the coccids, as suggested by VON IHERING, is indicated, not only by the fact the delicate sucking mouth parts of these insects are not adapted for excavating in dense tissues, but also by the fact that I have actually observed the ants in the process of excavating them.

Summary and conclusions

The theory of myrmecophily, as modified by SCHIMPER, interprets the structural peculiarities of myrmecophytic species of *Cecropia* as adaptations for enlisting the services of an aggressive army of Aztecas which protect their hosts against the attacks of the leaf cutting Attine ants. Cleverly conceived and suggestive as this Neo-Darwinian hypothesis undoubtedly is, it appears to be based upon a series of plausible deductions or teleological inferences, and is open to serious criticism. The distribution and feeding habits of the Attine ants in luxuriant, tropical forests are such that the ants are not likely to exterminate indigenous species. They show no strong preference for the foliage of *Cecropia*, and rarely attack either inhabited or uninhabited trees. Although Aztecas tend to prevent other ants from visiting the terminal portions of the adult Cecropias, they do not protect the juvenile individuals. That the curious prostomata and Müllerian corpuscles

of *Cecropia adenopus* and of other myrmecophytic species of *Cecropia* are not allurements, acquired through natural selection, is indicated by the fact that such structures occur on certain species of *Cecropia* and other plants which are not frequented by ants. The *Azteca-Cecropia* associations, and ant-plants in general, are extremely interesting cases of parasitism, which illustrate the remarkable adaptiveness of ants in availing themselves of the potentialities of given environments. This is shown, not only in the utilization of the preformed food bodies, prostomata, and internodal cavities, but more strikingly in the structural modifications produced within the plants for the growth and tending of coccids. Thus, the ants are able to obtain food from the plant in two ways, fats and proteins directly from the Müllerian corpuscles, and carbohydrates vicariously through the coccids.

I wish to thank WILLIAM BEEBE for numerous courtesies during my visit to the Tropical Station of which he is in charge. To the directors of the Gray Herbarium of Harvard University, the New York Botanical Garden, and the Berlin Museum, and to Dr. EMIL SNETHLAGE I am indebted for many helpful taxonomic data. These investigations were conducted under a grant from the American Association for the Advancement of Science.

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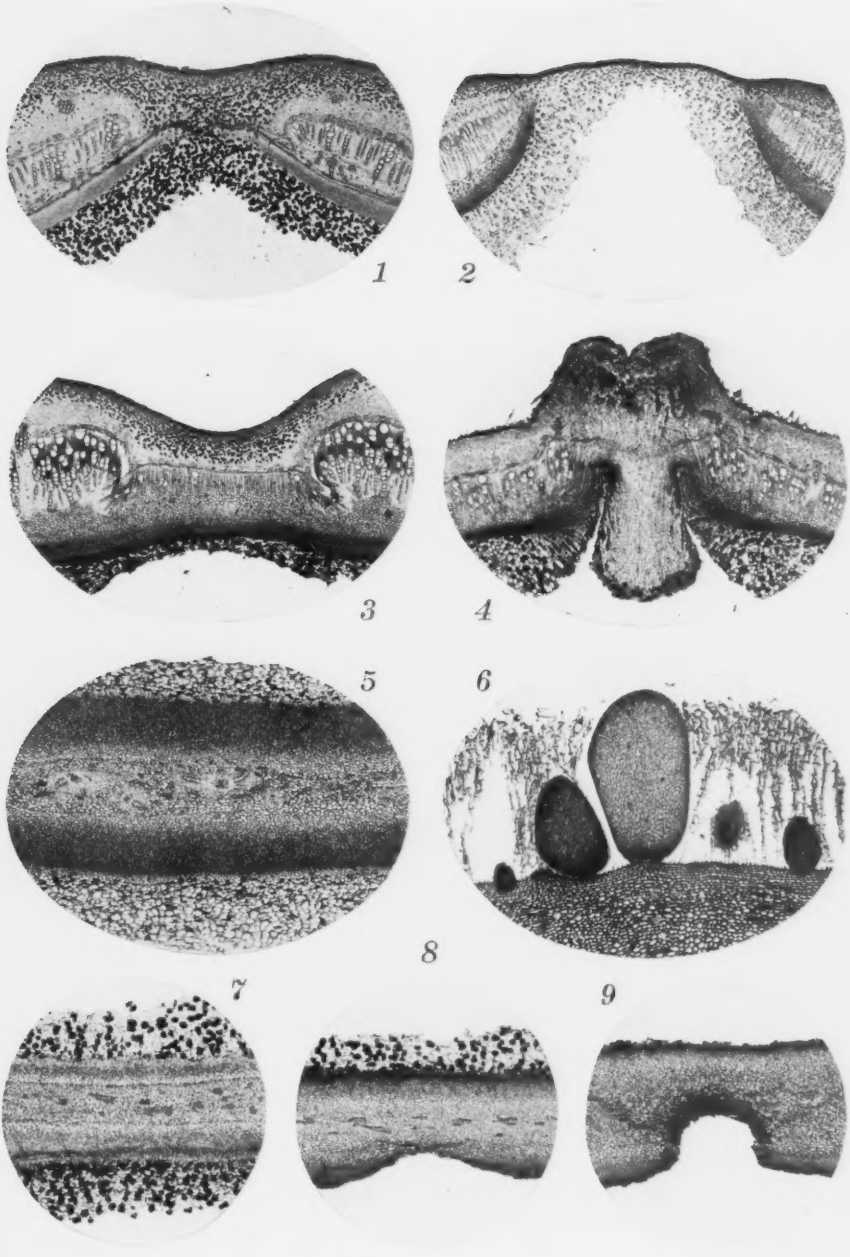

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EXPLANATION OF PLATE XV

FIG. 1.—*Cecropia angulata:* cross-section of upper portion of internode, showing "prostoma"; ×10.

FIG. 2.—*C. sciadophylla* var. *decurrens:* cross-section of internode, showing "prostoma."

FIG. 3.—*C. angulata:* cross-section of lower portion of internode, showing formation of secondary wood in "prostoma"; ×10.

FIG. 4.—*C. angulata:* cross-section of juvenile plant, showing occlusion of entrance aperture by callus or "stomatome"; ×11.

FIG. 5.—*C. sciadophylla* var. *decurrens:* cross-section of nodal diaphragm, showing five layers of three distinct types of tissues; ×18.

FIG. 6.—*C. angulata:* Portion of trichilium, showing food bodies and enveloping mat of hairs; ×43.

FIG. 7.—*C. angulata:* cross-section of nodal diaphragm, showing layers of thin walled parenchyma; ×11.

FIG. 8.—*C. angulata:* cross-section of nodal diaphragm, showing early stage in construction of a pitlike excavation; ×18.

FIG. 9.—*C. angulata:* cross-section of nodal diaphragm; soft external layers of medullary tissue removed on both sides, and circular perforation cut through horny layer on under side; ×15.

PROTHALLIA OF LYCOPODIUM IN AMERICA

II. L. LUCIDULUM AND L. OBSCURUM VAR. DENDROIDEUM

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 300

EARLE AUGUSTUS SPESSARD

(WITH PLATES XVI–XVIII)

In the first paper (4) there was included a short description of a single prothallium of *L. lucidulum;* also reference to what was thought at that time to be the prothallium of *L. obscurum* var. *dendroideum.* The question raised then was later settled in a short announcement published about a year later (5). It is the purpose of the present paper to describe fully the hitherto undescribed prothallia of these two species of *Lycopodium,* and to draw such comparisons as may seem justifiable.

Material and methods

The method of collecting described in the first paper has been followed almost entirely. It was found neither desirable nor practicable to sift or to wash the soil. The smallest desirable prothallia may be secured by the simple means of picking with curved forceps. A patch of soil in the form of a square or rectangle was removed to a depth of 4 or 5 cm., placed in a basket, and carried to the laboratory, where the prothallia were picked out. At frequent intervals small portions were placed under a dissecting microscope for the detection of the very youngest stages. Lying prone upon the ground is quite as good a method, save for the fact that one gets extremely tired after four or five hours of painstaking search.

For fixing, various mixtures of chromic-acetic-osmic acids were used, as well as formalin-alcohol. While the former proved to be somewhat better than the latter, it was not determined what is the best mixture.

The prothallia of *L. lucidulum* are ideal for a study of sex organs, since they are long dorsiventral plants with the organs mixed and growing acropetally from the apex. The main stages of both organs have been secured in a single section. This is rather rare, of course, but a comparatively few sections give one surprisingly good results. Since they can be secured very easily in the field because of their abundance, no other prothallia of *Lycopodium* offer so many advantages at once for class demonstration and laboratory material as these.

Lycopodium lucidulum

Since the prothallium of this species of *Lycopodium* was not known previous to my original brief description, it will not be out of place to give a rather detailed account of it.

Locality

Out of a total of more than 500 prothallia of *L. lucidulum* which were found, only about half a dozen were gathered outside the small region just north by several hundred yards of the Ridge Street Cemetery at Marquette, Michigan. Evidence of the existence of them was found at Mid-Island Point, Sugar Loaf Peak, Negaunee, Munising, Ishpeming, and Michigamme. There is no doubt that any region of the upper peninsula of Michigan will yield prothallia, providing, of course, that it is in general a habitat for the species. It is only because the present investigations were confined to a careful examination of a very limited region that a larger range cannot be given here. This limitation was made primarily to determine the relative abundance of material.

Occurrence

This species of *Lycopodium* produces prothallia in remarkable abundance. It is only necessary to become acquainted with the habitat and to exercise a due amount of patience and vigilance, to obtain a gratifying supply. All the prothallia were found within an area not more than 25 m. square. Within this area there were three especially rich patches, although these were not all discovered the same season. One was found in May, another in September, and the third in June of the following year. One patch measured

19 cm. × 16 cm. and yielded 153 prothallia; another, measuring 18 cm. × 14 cm., yielded 134 prothallia. The third patch was the most remarkable, being only 3 cm. square, and containing 74 prothallia. In the two larger patches there were 178 sporelings in all, 70 of which bore prothallia. Within the same general area in which the three rich patches of prothallia were found, were five other patches of the same general size, but which produced only sporelings. No effort was made to count them, but they were more numerous than the prothallia themselves, and were so closely crowded that many of them failed to produce more than the first set of leaves. In searching it was found to be much more profitable to seek patches of abundant sporelings than to wander about looking for isolated groups of them, even though these patches often failed to produce any prothallia in spite of the great number of sporelings. From this abundance of sporelings it is evident that not infrequently prothallia occur in even greater quantities than were actually secured from the richest patch found.

Relationship to spore-bearing plants

This investigation confirms the experiences of others who have found prothallia of *Lycopodium*, namely, that they occur most frequently where adult sporophytes are scarce. It seems probable that this situation must be explained by some difference in the soil. Since we know nothing of the conditions which govern the germination and development of *Lycopodium* spores, so far as the soil is concerned, a certain answer to the question is impossible. I have observed, however, that the soil in which prothallia grow is drier than that in which the adult sporophytes are found. This is especially true for the species under consideration. It is certain that an enormous number of spores must find their way to the soil beneath the cone-bearing plants, but the latter grow so thickly that sporelings would have little chance of survival, granting that prothallia had succeeded in growing. The sickly condition of many of the thickly growing sporelings found supports this idea.

As a matter of fact, prothallia do occasionally occur in even the densest growths of adult sporophytes, and it is not improbable that they might be found there in quantity. The fact that investi-

gators consistently fail to uncover prothallia with adult sporophytes where the latter are growing thickly, in the opinion of the writer does not negative the probability, for it is most tedious to hunt the plants under these conditions. BRUCHMANN (1) has investigated old areas of sporophytes probably more carefully than any other investigator, but his method was first to remove the adult plants and then to look for sporelings. In doing this the majority of them would be destroyed. The writer has investigated the older plant areas, both by the method of BRUCHMANN and without first removing the adults. Four prothallia were found by the latter method and none by the former. Since the chief object was to secure prothallia, the waste of time necessary to secure only a few specimens among adult sporophytes caused the writer to abandon such areas.

The question naturally arises as to how the adult plants of *L. lucidulum* reach the habitats which are more moist than that of the prothallia. Let us assume that a prothallium has succeeded in growing on the side of a knoll or a hill, and that at the bottom of this knoll or hill is a moister habitat favorable for the growth of adult sporophytes. When the sporeling breaks through the surface of the ground it faces the hazards of drought and too much sunlight. If these are simultaneous or of sufficient duration, the plant must surely die. The observations of the writer are that this is a constant catastrophe in the struggle of these delicate plants. Occasionally, however, we may expect to find a plant growing under the conditions of a wet season. Then it progresses rapidly and becomes a hardy specimen. When it becomes an adult it is capable of producing spores and gemmae. It seems likely that it is the gemmae that play the chief rôle in further distribution, for when small clusters of these adult plants are found they almost invariably bear numerous gemmae, but rarely sporangia. When the gemmae fall in habitats favorable for the growth of prothallia, they may germinate well, and even form normal sporelings, but it is a significant fact that they appear unhealthy and generally show the incipient stages of extinction. On the other hand, those that reach a moister region, like that at the bottom of our assumed knoll or hill, grow vigorously.

The line of distributive succession is not easily shown in *L. lucidulum*, but a case of *L. obscurum* was found that well illustrates the idea. A sporeling of this species was found that was 10 cm. long, bearing six successive aerial branches and a distinct foot at the end of the underground trailing stem. The sporeling grew on the top of a small knoll, but instead of staying there, it took the shortest path toward the bottom, where adult sporophytes were growing in a moist hollow.

The rôle of prothallia in the life history of *L. lucidulum* is of slight value to the species, therefore, once a colony is firmly established. But for the opening up of new localities, and therefore for the geographical distribution of the species, the gametophyte plays the important part of getting a foothold in regions too unfavorable for vegetative parts, especially gemmae, to flourish. The sporeling itself rarely reaches maturity.

Two facts were observed in the collection of prothallia of various species which seemed to indicate that some agent other than wind takes part in the distribution of spores. The first of these was that the prothallia, in nearly all species, occur in bunches. The second was the frequent occurrence of prothallia in groups of four. The latter condition is explained by supposing that the original group of tetraspores was distributed bodily, and that the four germinated simultaneously. This phenomenon was observed very frequently in *L. clavatum*, *L. complanatum*, and *L. lucidulum*, most frequently in the first.

At the time of the shedding of spores the tetrasporic group is broken up, so that it does not seem probable that these groups are distributed by the wind. The only other explanation which suggests itself is that portions of the plant bearing sporangia are carried away by animals. The appearance of patches of prothallia and sporelings strongly suggests this. An isolated sporeling or gametophyte is rarely found.

HABITAT

Many searches for prothallia have been futile, not so much through a paucity of material as through a failure to learn, by a process of elimination, the exact type of terrain in which they grow

most abundantly. It is difficult to describe what this is. In general one must follow the same principles involved while searching for the prothallia of any pteridophyte group.

For the prothallia of *L. lucidulum*, moisture is without doubt the most important factor. Countless millions of spores shed annually from an acre of these plants fail to produce prothallia, either because they are washed away into streams, driven too deeply into the soil, lodged in water logged depressions, or are subjected to dry conditions before and after germination. It is only when they fall upon a region whose sandy substratum is covered by a thin layer of leafmold, and is sufficiently protected from the seasonal drought and from inundation, that they germinate and produce prothallia. Such a place is a hillside or a hilltop with scattered trees, very little shrubbery, and a scattered representation of such herbs as the squawberry, wild sarsaparilla, *Clintonia borealis*, and *Polygala*. Very often grasses and *Polytrichum* are found in such a habitat. A sandy knoll with sparse vegetation and with a swamp at its base is an excellent locality.

BRUCHMANN found many of his prothallia of *L. Selago*, a related species, in mats of moss. The writer found very few in such places. The rich patches just described lay on a sandy hillside and were protected only by the leaves which fell the previous autumn. The soil was a rich humus for a depth of 1 cm., with almost pure sand beneath. Although hundreds of sporelings were found, many were in a desiccated condition, and only a very few would ever have become adults, for adult plants habitually occur in regions a little more moist than where the prothallia and sporelings were found.

Because the prothallia of this species of *Lycopodium* were found growing in such a variety of places, the following list of these may be valuable: (1) in a hole at the base of a living birch tree; (2) among the decayed needles of *Pinus resinosa;* (3) under a hard maple tree; (4) on the top of a rotten stump; (5) on partly shaded hillsides; (6) in the sand under a patch of *Polytrichum* and *Polygala;* (7) in sand scarcely covered at all with humus; (8) in moldy humus (most abundantly); (9) in muck, at the edge of a permanent pond; (10) in the wheel tracks of an abandoned forest road.

It might be well to add that the habitat of the prothallia of this species of *Lycopodium* is somewhat more shaded, more moist, and more protected from sunlight than that for *L. clavatum*, *L. complanatum*, and *L. annotinum*. The prothallia of five species have been found within a few centimeters of each other, however. They are most abundant at a depth of 1 cm., and seldom grow at a depth of more than 2 cm. Very frequently they occur upon the surface of the ground. The habitat of these prothallia agrees in all essential respects with that for *L. Selago*, with the exception already mentioned, which seems to indicate that they require a slightly drier place for growth than do those of the latter.

DESCRIPTION

The older regions of the prothallia are brownish, while the young growing tips as well as the very young prothallia are white. It is these very white tips that are first noticeable when digging in the soil. They are closely beset with multicellular hairs (fig. 49), which in some cases include as many as five cells. They are evidently of a glandular nature, for in fresh specimens of prothallia the region which bears them is covered with a thin mucilaginous secretion slightly denser than water. If the prothallia are placed in water, this substance quickly swells and is dissolved. Whatever its nature, no doubt it plays the important rôle of keeping the young growing region and the young sex organs from becoming dried. None of the fungus filaments which closely adhere to the exterior of other parts of the prothallium ever pierce it, nor do soil particles or leaf mold adhere to it. It is probable that the growing apical region is lubricated sufficiently by this substance to prevent injury during its upward passage through the soil and mold, which are often very compact and solid.

The adult prothallia vary very much in size and shape (cf. figs. 2–41). These figures are all drawn to a scale of four, so that they are just twice the size of the original specimens.

The form of the prothallium does not conform exactly to that of any type heretofore described. It approaches nearest that of *L. Selago* described by BRUCHMANN. Taking fig. 15 as the type form, it will be noticed that there is a lower cup-shaped primary

region, from which has developed a more or less dorsiventral protuberance which becomes cylindrical near its apex only. In no case were there found the two forms of body as described for *L. Selago*, namely, the cylindrical or "ninepin" form and the flattened form. All the specimens of the vertically growing prothallia of *L. lucidulum* might roughly be considered as shaped like a "ninepin" or an Indian club, but upon close examination it has been found that sex organs grow only on one side, the rhizoids opposite and lateral to them, and that the symmetry is distinctly dorsiventral. It is only when active growth is taking place that the apical region ever becomes cylindrical at all. Fig. 51 shows a longitudinal section through the apex of a prothallium such as that shown in figs. 15 or 49. This bilateral symmetry is present from the very beginning of the differentiation from the meristem tissue.

If the prothallia grow upon the surface, however, they are distinctly of the *L. clavatum* or *L. annotinum* type (figs. 33, 35). Even when growth continues after a subterranean prothallium has reached the surface, this growth produces an expanded portion which rests upon the ground (figs. 34, 37, 39). In other words, when the length of the vertical portion is eliminated so that the primary tubercle lies immediately beneath the prothallium, we have a type in no essential respect different from that of *L. annotinum*. Figs. 32 and 37 show prothallia semisurface and semisubterranean in development. In many instances (figs. 25, 28) horizontal growth is solely below the surface, and it is not until near maturity that the apical point turns abruptly vertical. In such instances the prothallia are evidently of the *L. annotinum* type originally, and later change.

In short, there are three methods of growth: one in which growth is entirely vertical; one in which growth is first vertical, then horizontal; and another in which growth is first horizontal and then vertical. In several instances growth was originally vertical, later assumed the horizontal, and still later resumed the vertical.

While a prothallium of *L. Selago* has never been examined, I cannot see from the figures of BRUCHMANN any evidence of a typically "conical" or "ninepin" shape for that species of prothallium. His fig. 32, plate VI, is the nearest approach to it, but the form is

far from being typical, as the drawings to the left of it show. Even in fig. 32 the sex organs occur on one side, while the vegetative organs are mainly opposite and lateral to it. Apparently the only difference between the form of the prothallia of the two species in question is the alleged conical shape of *L. Selago* prothallia, and I am not able to see that BRUCHMANN'S figures admit even of this difference. If I were to use the same method of drawing as he has, it would be almost impossible to distinguish between the typical forms of prothallia of the two species. BRUCHMANN'S figs. 22, 28, and 29 are especially easy to match with prothallia of *L. lucidulum*. My figures merely accentuate the different regions of the prothallia, while his suggest them.

For the present, therefore, the prothallium of *L. lucidulum* is placed with BRUCHMANN'S type for *L. Selago*, but it is probable that the necessity for such a type is one of convenience rather than a morphological one. For the sake of reducing the growing number of types of prothallia for the genus *Lycopodium*, it might be well to include these representatives of the *L. Selago* type in the *L. clavatum* type.

Chlorophyll occurs regularly and abundantly in the subepidermal cells of all prothallia of *L. lucidulum* which were found growing upon the surface. Four prothallia were found which had bifurcated. The age of the prothallia varied greatly, as the figures show. There seems to be some evidence that the prothallia of *L. lucidulum* have a much shorter period of development than BRUCHMANN found for his European species. Solely from field observations I should estimate that adult prothallia for *L. lucidulum* probably mature within two or three seasons, but the period for *L. obscurum* must be much longer.

TISSUES

A longitudinal section of a prothallium like that shown in fig. 50 shows two main regions, an upper and a lower. The upper region is divided into a distinct epidermis, which bears the sex organs and paraphyses, and a subepidermal mass of cells of parenchymatous structure which contain chlorophyll (when this is present) in its upper half and reserve starch in the lower half. A cross-section is shown in fig. 64. This set of tissue, therefore, is reproductive

and assimilative in function, in its upper portion, while its lower portion is employed for the storage of food material. The starch grains are compound. While they occur most abundantly in the lower half of the upper set of tissues, very frequently they are found also in the cells immediately below the epidermis, in the venter of the archegonium and the cells of the fungus regions (fig. 64). Approximately the lower half of the prothallium is inhabited by the endophytic fungus. This will be described later.

The meristematic tissue (figs. 51, 52) lies at the apical end of the prothallium in a depression between the two groups of tissues just named. A single apical cell is probably not present. Growth is apparently brought about by periclinal and anticlinal division of a small number of cells which form a meristematic plate between the youngest portions of the upper and lower sets of tissues. The mitotic figures of fig. 51 show that division continues in cells which lie at a considerable depth. The lobed-like mass of tissue which bends downward over the apical region and which bears the primordia and older cells of the sex organs is caused by this division of the interior cells, as well as by the rapid division of the more superficial ones. The cells of the meristematic plate, from which are cut off immediately the vegetative and reproductive primordia, are filled with dense protoplasm and numerous oil drops (fig. 53).

Rhizoids are very abundant, and are simple elongations of epidermal cells on the lower side. No case was observed in which a rhizoid was cut off by a cross wall.

Sex organs

The prothallia are monoecious. The sex organs appear in acropetal succession (fig. 51), the older ones being located (fig. 50) in the tissue lying above the primary tubercle. Both antheridia (figs. 54–58, 62) and archegonia (figs. 42–47) develop by the usual stages known for the genus. The largest number of canal cells found was four. A double row of these was not observed. The ventral canal cell is very much flattened at maturity. The egg is slightly oval at maturity, with the long axis perpendicular to the canal. It almost completely fills the venter. The neck of the archegonium is short, and the venter lies completely below the

level of the epidermis. The neck is not provided with a cover cell. It opens by the dissolution of the inner walls of the four terminal cells which border each other at a common line. As soon as fertilization takes place further development of archegonia normally ceases. Consequently two embryos on the same prothallium are rarely found, and since fertilization occurs after the opening of the canal, the embryo therefore lies very near the meristematic region. The growth of the embryo causes activity there to stop, and as a result it is found as a rule at the end of the prothallium.

Antheridia appear earlier and more abundantly than archegonia, and are scattered throughout the entire upper surface of the prothallium. They are circular or oval in outline, and may be submerged entirely or may form a slight elevation on the upper part of the prothallium. They are isolated and never form antheridial masses similar to those very characteristic of *L. obscurum* to be described later. Figs. 58 and 59 show the latter stages in the development of the sperm.

The sex organ primordia lie so close together that it is impossible always to say what kind of organ will develop. They may be separated by a single layer of cells, or, as Miss LYON (3) observed in *L. annotinum*, they may touch one another. They are evidently of such a primitive nature that it is impossible to distinguish an antheridium from an archegonium in the very earliest stages of their development. There are some indications that the archegonial initial is slightly larger and longer than the antheridial initial, but this is so uncertain that it is useless as a criterion.

As a result of this primitive condition, mixed sex organs are very frequently found. These may be normally shaped antheridia in which a few cells have never divided into sperm mother cells, or they may be archegonial in form, the neck filled with normal spermatogenous tissue, and the ventral canal and egg cells of female appearance (fig. 60). The opposite condition may also occur (fig. 61). Figs. 60 and 61 are sketches of two archegonia constructed from camera drawings of nine sections in serial order. Six abnormal organs of a bisexual nature were found on one prothallium. They of course always occur near the apex of the prothallium. The fact that sexual organs of a bisexual nature occur

on plants where primordia of sex organs are apparently alike in position, suggests that we may be dealing with one of the primitive stages of sex organ development. HOLFERTY (2) found the same indifferent situation in *Mnium cuspidatum*. Miss LYON brought together considerable information on several genera of pteridophytes regarding the condition in abnormal archegonia. A longitudinal section is best for the study of sex organs.

Only the first division in the development of the prothallia from the spore was observed. Fig. 1 illustrates the single specimen which was found in field material.

Lycopodium obscurum dendroideum

The prothallia of this species were most difficult to find. The sporelings have an appearance so much like those of *L. complanatum* that a certain abnormally growing prothallium of the latter species was described in my first paper (4) as that of *L. obscurum*. This error was corrected as soon as discovered (5). A total of thirty-seven prothallia were found. Twelve were dug up in a patch 2 feet square near the locality described for *L. lucidulum*, and very near to a juniper bush. The others were found near Mid-Island Point, Michigan. The exact spot lies just behind a row of cottages, about 300 yards from Lake Superior and in an alder clump between the lake and the marsh to the east of it. This spot was visited first in July and later in August of 1917. It was very dry at this time, but is probably water-logged for at least two months of the year. Twenty-five prothallia of *L. obscurum*, fifteen of *L. complanatum*, and six of an undetermined variety of *L. clavatum* were found in an area not more than 10 feet square.

The soil in the first locality contained very little humus in the sand. A species of grass and *Polytrichum* grew about the spot, which was fully exposed to the sun, and no leaf mold was present. The sand was yellowish a short distance below the surface, and rather compact. The spot rests on a ridge about 15 feet higher than the surrounding land. The lake bed once covered this point, and it is probably an old sand bar.

The soil of the second locality could hardly offer a more contrasting condition as to physical appearance. The subsoil of course

was sand, but this was covered by a soil mixture of half leaf mold and half muck, covering lake sand. As a matter of fact, some of it was nearly pure mycelial threads. Other parts were as hard as dry muck itself. The prothallia found here grew for the most part in the intensely moldy soil. Some were found at the border between the humus layer and the sand lying beneath it. From this it will be seen that one cannot name a type of soil as a criterion.

If it is desirable to indicate the type of place to look for *Lycopodium* prothallia, I should say that one should look in neither the dry nor the wet places. For my own part I search in those spots a little less moist than the habitat of the adults. In the case of *L. obscurum* and *L. clavatum*, very often the reverse is true, but just as one cannot give a precise type of soil and moisture content for the sporophytes, so he cannot for the gametophytes.

Sporelings were found in a variety of other places near Marquette and Munising. The prothallia of *L. obscurum* probably grow abundantly wherever the sporophyte has been known to exist for a long time and in considerable quantity. Two prothallia and one sporeling were found in July 1922, near Rhinelander, Wisconsin. A sporeling and an old prothallium of *L. complanatum* were found in June 1922, near Pembine, Wisconsin.

Description of prothallia

The prothallia are of the *L. annotinum* type and not of the *L. complanatum* type suggested in my first paper (4). They are about as smooth as the *L. annotinum* prothallia, and never as wrinkled or lobed as those of *L. clavatum*. While the first are yellowish brown and the second dark brown, those of *L. obscurum* are reddish brown. They are also somewhat larger than those of the other species. The largest one found measured 8×12 mm.; the smallest was about the size of a pin head. Figs. 65 to 71 show them just twice the natural size. Owing to the fact that the rhizoids are so few that the soil scarcely clings to them, they may be distinguished by this means also. The young of the three species just mentioned and *L. complanatum* cannot always be distinguished, but identity of species can generally be determined by the habit of growth of the endophytic fungus. Confusion of species is sometimes

unavoidable, however, and this is especially true when prothallia of several kinds and of young age are found in the same lump of soil. The writer discovered such a mistake after a four months' study of a single slide. Certain features relative to the fungus were found on it that did not occur in any of the other specimens to which it purported to belong. In fact, it was this discrepancy that led to the discovery of the mistaken identity of the prothallia under discussion. The habit of growth of the endophytic fungus will be discussed later.

Fig. 70 shows a specimen of *L. obscurum* which looks like *L. complanatum*. The color and endophytic fungus both place it with the species assigned. Furthermore, the remarkable habit of growth of the antheridia was found present here, although the drawing does not show it. The enlarged antheridial mass shown in fig. 81 was taken from a specimen of a large *L. complanatum* prothallium. Both were rotted away at the lower end. Now no published figure of the last named species of prothallium shows that antheridia grow in such enormous masses. These facts can mean only one of two things, namely, that the fact of antheridial mass growth has not been observed, or that the form of *L. obscurum* prothallium is really intermediate between the *L. complanatum* and *L. annotinum* types. In view of the fact that other observers of *L. complanatum* prothallia were unlikely to overlook so conspicuous a feature, I am inclined to the view that the prothallia of *L. obscurum* occasionally take the intermediate position between the two well known types. After careful examination of the specimens found there is small likelihood of mistaken identity. If this be true, what I have called a prothallium of *L. obscurum* in my first paper (4) may need no modification. Moreover, the prothallia of *L. Selago*, *L. lucidulum*, and the peculiar specimen of *L. obscurum* all show a lateral groove more or less extensive, and are dorsiventral.

Sex organs

The antheridia grow in enormous masses of white beadlike knobs. These may half encircle the entire prothallium in the adult, or may cause the very young to resemble cornucopiae. Such structures have not been observed by the writer on any other pro-

thallia with certainty. Certain prothallia previously figured (4) seem to suggest them, but at that time prothallia of *L. obscurum* were unknown, and identification was made upon comparison with figures published by other writers. It is entirely possible that those specimens may have been misnamed. There is also the possibility that antheridia may occasionally take the form mentioned in species other than the one under discussion. Figs. 79–81 show the habit of growth of these organs. The prothallia are all shown under a magnification of ten, so that a glance at the figures will give the relative size of the individuals figured. Fig. 81 shows a mass enlarged.

A cross-section of the prothallium through two antheridial ridges is shown in fig. 74. It is apparent that the masses arise from the tissue lying within the outer border ring. For sake of clearness, one region is represented as without the endophytic fungus. As a matter of fact the fungus does invade the antheridia through the opening shown by the opercular cells in figs. 82 and 89. It has not been located for certain in the cells of the antheridia walls, but it is possible that the fungus is present in the intercellular spaces. Because of the intimate relationship between the sperms, and possibly the wall cells, with the fungus, it seems very likely that the unusual growth of antheridial masses may be explained by symbiosis. There is no indication of a pathological condition of the sperms. The writer has never seen the fungus in the antheridia of any other species of prothallia of *Lycopodium*. It is well known that an endophytic fungus present in the prothallia of certain ferns will cause abnormal growth of tissue.

The individual antheridia arise acropetally from the groove. There is no primordium for the mass. This is a secondary growth, although it arises very early. Figs. 87 and 88 show the antheridium initial and the first division. The mature detail is shown in figs. 82 and 89. In this species four opercular cells may often be observed. I have never seen it for certain in any other species. The figures representing these cells were made by camera lucida.

In all of the prothallia sectioned, numerous retarded antheridia were observed. They were distributed throughout the older regions of the plant, and had the ordinary appearance of the male organs,

but the mother cell walls were extremely weak and the nuclei small. They appeared starved. The endophytic fungus was not demonstrated to be present in them, and it is very probable that they originated in the usual way.

Mitosis does not occur simultaneously throughout the individual antheridia. The organ is divided into quarters, and all the cells of a single quarter will show the same phase, but one earlier or later than the neighboring quarter.

Archegonia

The stages in the development of individual archegonia are the same as those described for the genus. A few of the stages are shown in figs. 83–86. The neck is rather long, containing as many as fourteen canal cells. As a rule these are double, or at least part of them are. Even the ventral cell is involved in this division (fig. 86). In this organ the cells are beginning to disintegrate, as shown by the swollen walls. The position of such an organ relative to the prothallium is shown in fig. 90 on the cut edge. That the doubling of the neck canal cells occurs early is shown by fig. 85. One instance was observed of a very abnormal archegonial growth. Six organs arose from the prothallium (fig. 90), which were all apparently normal, near maturity, and about the same age. There were traces of the endophytic fungus in the canals. The fungus occurs normally in all the archegonia. It is probable that this peculiar massing of archegonia is to be explained on the same grounds as the antheridial masses. It would be instructive to know how frequently this occurs. Unfortunately the mass was not discovered until sections had been made, and the topographic view had to be made up from serial sections.

The exact morphological position of the sex organs, especially the antheridial masses, should be made plain. From a superficial view of fig. 80, it might appear that the upper mass is derived from the border, but the section shown in fig. 74 should make the matter clear. It was rather difficult to determine the origin of the mass. Antheridia of all ages are found in any one, but the primordia always are found at the outer junction of the mass and the prothallial tissue beneath. Nevertheless, certain sections showed that the

primordia were slightly raised above the surface, as though dragged there by rapid growth of the surrounding tissue. While I am satisfied that there is no definite primordium for the mass, I am not at all certain that the mass itself may not begin development before the antheridial primordia appear; at least convincing evidence was not found. If the fungus is responsible for the growth, almost any order may be expected in the development of some individual organs. It was not possible to be certain of the relationship between the developing mass and the developing antheridia. The organs are so numerous that only one of two things can occur, either the whole group must spread itself, or most of the individuals must be absorbed. There is conclusive evidence in the figures that few are absorbed.

Endophytic fungus

The study of the endophytic fungus has delayed the publication of this paper considerably. The following account refers to that found in the two species of prothallia under discussion. Plate ∞ has been added to show some of the structures observed. The identity of the fungus has not been established. It does not appear to be the same in both species. Both the reproductive structures and the habit of growth support this statement. Furthermore, there is evidence that they may both be Ascomycetes.

The illustrations are arranged so that the fungus of *L. obscurum* is represented in the upper half of the plate (figs. 91–110), and that of *L. lucidulum* in the lower half (figs. 111–126). Each group is subdivided into reproductive and vegetative structures. No attempt has been made to insure the morphological identity of any structure represented. In the *L. obscurum* group, figs. 94–105 are supposedly reproductive structures, and figs. 106–110 vegetative. In the *L. lucidulum* group, figs. 113–117 and figs. 122–126 are supposedly reproductive, while figs. 118–121 are vegetative. The structures shown in figs. 124 and 125 were found in both types of prothallia. They are all shown under the same magnification, and are collected from over 500 drawings.

All the reproductive structures, except in figs. 124–126, were intracellular. The vegetative structures were intercellular. The

ascomycetous growth of fig. 124 was very common, but always was found just outside the epidermis. It was found connected with the intracellular mycelium, however. The mass shown in fig. 125 was often observed in decayed regions of the prothallia. Since the "spores" shown in fig. 126 were found in such a mass, it is probable that the fungus sometimes destroys the prothallium in the older parts, to distribute its own spores. At any rate, many prothallia of *L. complanatum* were found with the entire lower half rotted away, and all the prothallia of *L. obscurum* sectioned, and a few of *L. lucidulum* had rotten holes in them which were filled with the fungus.

Habit of growth

The fungus enters the prothallium either through the rhizoids or between the epidermal cells. To say that it enters is not exactly accurate. It may be possible to show that many of the "entering" mycelia are in reality leaving the prothallium. It undoubtedly gets a foothold during the earliest life of the plant. To within two or three cells of the meristematic cells it is established (figs. 50, 51), which shows that it is eminently capable of taking care of itself, once it has obtained a foothold.

In *L. lucidulum* the fungus occupies the region shown in fig. 111, but there is one peculiar thing to be noted. Only about half of the cells contain the mycelial threads, the other half contain bodies which in some respects resemble spores (fig. 112). These show no nuclei under various stains. With safranin and aniline blue the walls reacted like cellulose. In a few cases minute red chromatin-like granules appeared differentiated, but these were never seen after iron alum haematoxylin; consequently, it is impossible to state just what these bodies actually are. In a few instances very minute mycelial threads were seen to radiate from pores in the walls of these bodies, as though they were germinating spores. These were always seen in section and cannot alone be considered conclusive evidence that they are indeed such structures. So far as this investigation goes, it cannot be said that they do or do not have any relation to the endophytic fungus. They are such a constant structure associated with the fungus, however, that some

connection seems extremely probable. One other fact should be noted. The obviously reproductive structures, found abundantly in the cells which lie next to those containing the sporelike bodies, are found without these sporelike bodies in the region neighboring the meristematic tissue. In other words, the sporelike bodies are not found in the cells which abut the meristematic cells. Since the structures which looked like germinating spores and appeared to contain chromatin also appeared in those very cells where the typical sporelike bodies were wanting, the evidence is still stronger for the spore interpretation. A few microchemical tests were made to determine the exact nature of the cell wall of these bodies, but nothing definite was established.

In *L. obscurum* the habit of growth of the fungus is markedly different. The reproductive bodies are larger, and there are none of the small sporelike bodies so persistent in *L. lucidulum*. All the cells of the infected region contain the mycelium, but it is much less extensive than in *L. lucidulum* (figs. 91, 93). Here there are two lower cells with a very regular and tight coil of the mycelium, which is much denser than shown in the illustration, where clearness was desired. Above this layer is a region of finer coils, generally about one cell in thickness. The coils change their orientation slightly in the next layer above, until those of the uppermost layer are at right angles to those of the lowest layers. The reason for this is probably one of absorption, for the mycelial threads finely divide and closely abut the walls of the palisade tissue which lies above and which contains reserve starch. These fine threads were never observed to enter the palisade cells, nor did their tips show swelling. This very evident difference in habit constitutes my first reason for believing that the fungus in the two species of prothallia under discussion is not the same. The second reason involves the reproductive-like structures. A glance at these structures at the top and bottom of the plate will reveal organs drawn to the same scale, but vastly different in detail. The only possible comparison may be found in figs. 97 and 125. The latter may be only a later stage of the former. The lefthand cell of fig. 112 when compared with fig. 97 shows the contrast well. The organs of the last named figure occur only in the lower cells of fig. 93, but

those of fig. 112 are equally distributed over the fungus region of *L. lucidulum*.

In spite of these observations, there is another which needs to be noted, and which may cast doubt upon them. The structures shown in fig. 124 were found on the epidermis of both kinds of prothallia. That shown in fig. 125 was never found except in the decayed portions of both kinds of prothallia. I suspect that the latter is only the maturer stage of the former. The "spores" of fig. 126 were drawn from a ruptured heavy walled structure shown in the lower lefthand corner of fig. 125. There were sixteen spores. All these facts point to the ascomycetous nature of the fungus, but since these last named structures were all found without the epidermis or within decayed regions where external fungi would have access, it is conceivable that they have no relation whatever to the endophytic fungus. The internal mycelium was so constantly segmented, however, that the Oomycete group has little chance of being recognized.

While the evidence presented is in no respect conclusive, it throws some doubt upon the *Pythium* theory as to the identity of the endophytic fungus of *Lycopodium* prothallia. The writer dislikes very much to leave so important a question unsettled, but it seemed best at least to record what had been observed.

Summary

1. The prothallia of two more species of *Lycopodium* have been discovered.

2. The sex organs of *L. lucidulum* are primitive, being frequently mixed in nature.

3. The prothallium of *L. obscurum* var. *dendroideum* shows a form transitional between the *L. annotinum* and *L. complanatum* types.

4. The sex organs of the last named species are invaded by the endophytic fungus and consequently show deformities. The antheridia and rarely the archegonia occur in enormous masses.

5. The sex organs develop individually as described for the genus, and acropetally in the two species.

6. The endophytic fungus is probably not *Pythium*. The reproductive structures point to this genus, but the vegetative and certain doubtful structures point to the Ascomycetes.

7. The habit of growth, and the appearance of the reproductive structures, indicate that the same species of fungus is not present in the two prothallia.

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EXPLANATION OF PLATES XVI–XVIII

PLATE XVI. PROTHALLIA OF L. lucidulum

FIG. 1.—Germinating spore, with first wall transverse; found in field.

FIGS. 2–41.—Habit sketches of various typical prothallia, some of which bear sporelings attached; ×2.

FIGS. 42–48.—Stages in development of archegonium; ×375.

FIG. 49.—Tip of prothallium, showing five antheridia and multicellular hairs.

FIG. 50.—Longitudinal section of prothallium.

FIG. 51.—Apex of same, showing acropetal succession of sex organs; meristem plate of cells lies just behind first initial.

FIG. 52.—Detail of meristem and initial plate; ×375.

FIG. 53.—Single cell from meristem region; ×775.

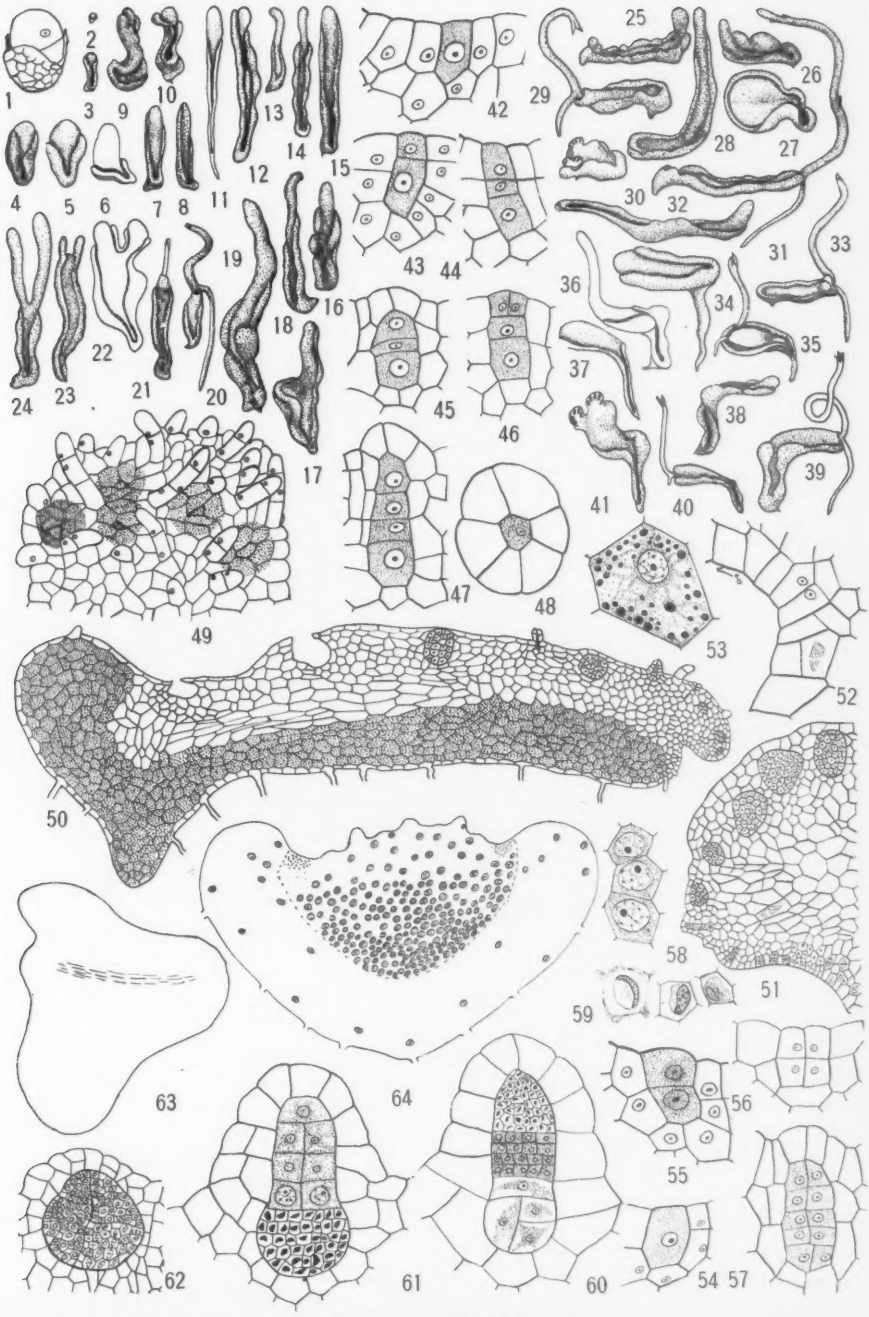
FIGS. 54–57, fig. 62.—Stages in development of antheridium and sperms; ×375.

FIGS. 58, 59.—Stages in sperm development; ×775.

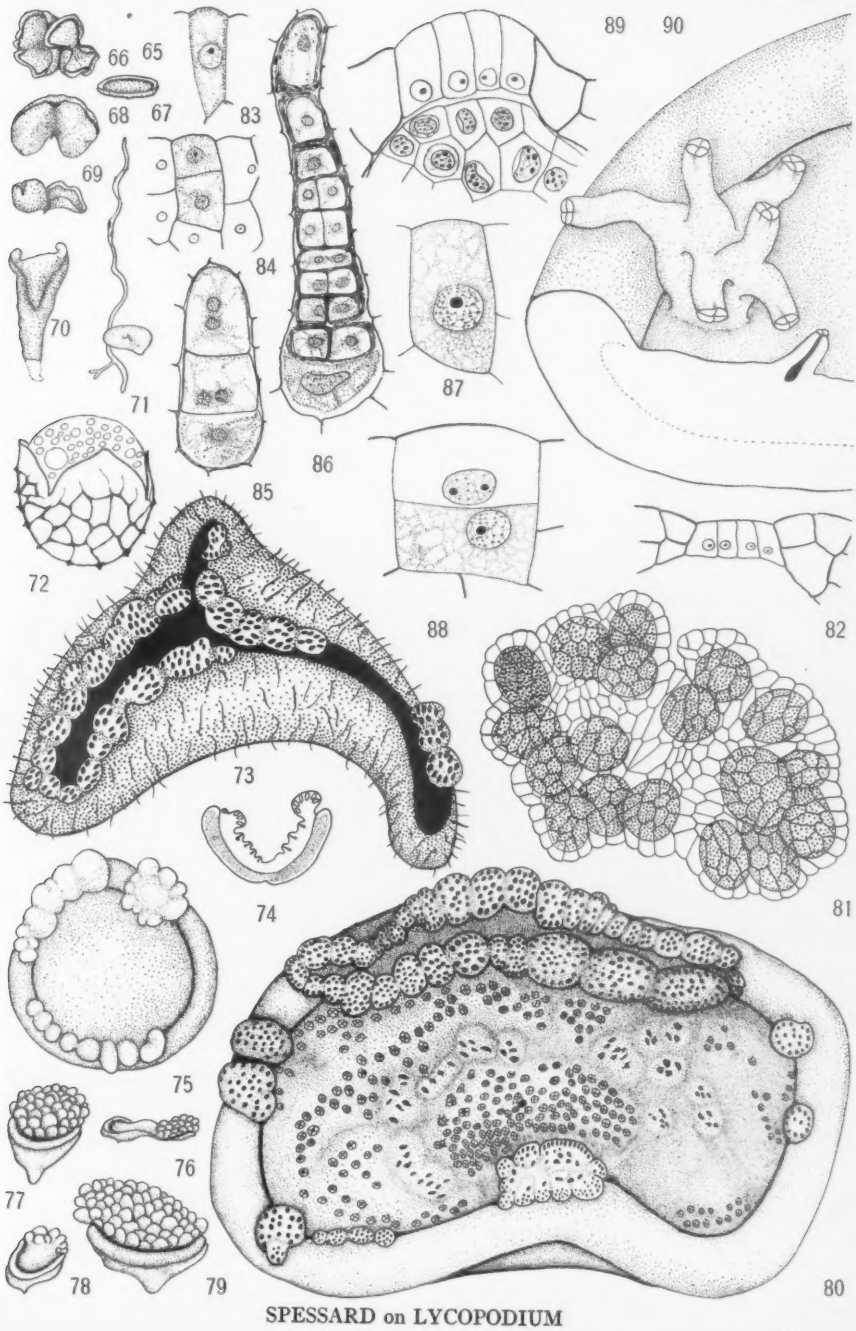
FIGS. 60, 61.—Mixed sex organs, reconstructed from serial camera drawings; ×375.

FIG. 63.—Longitudinal section of embryo; ×85.

FIG. 64.—Cross-section of prothallium, showing distribution of starch grains.



SPESSARD on LYCOPODIUM



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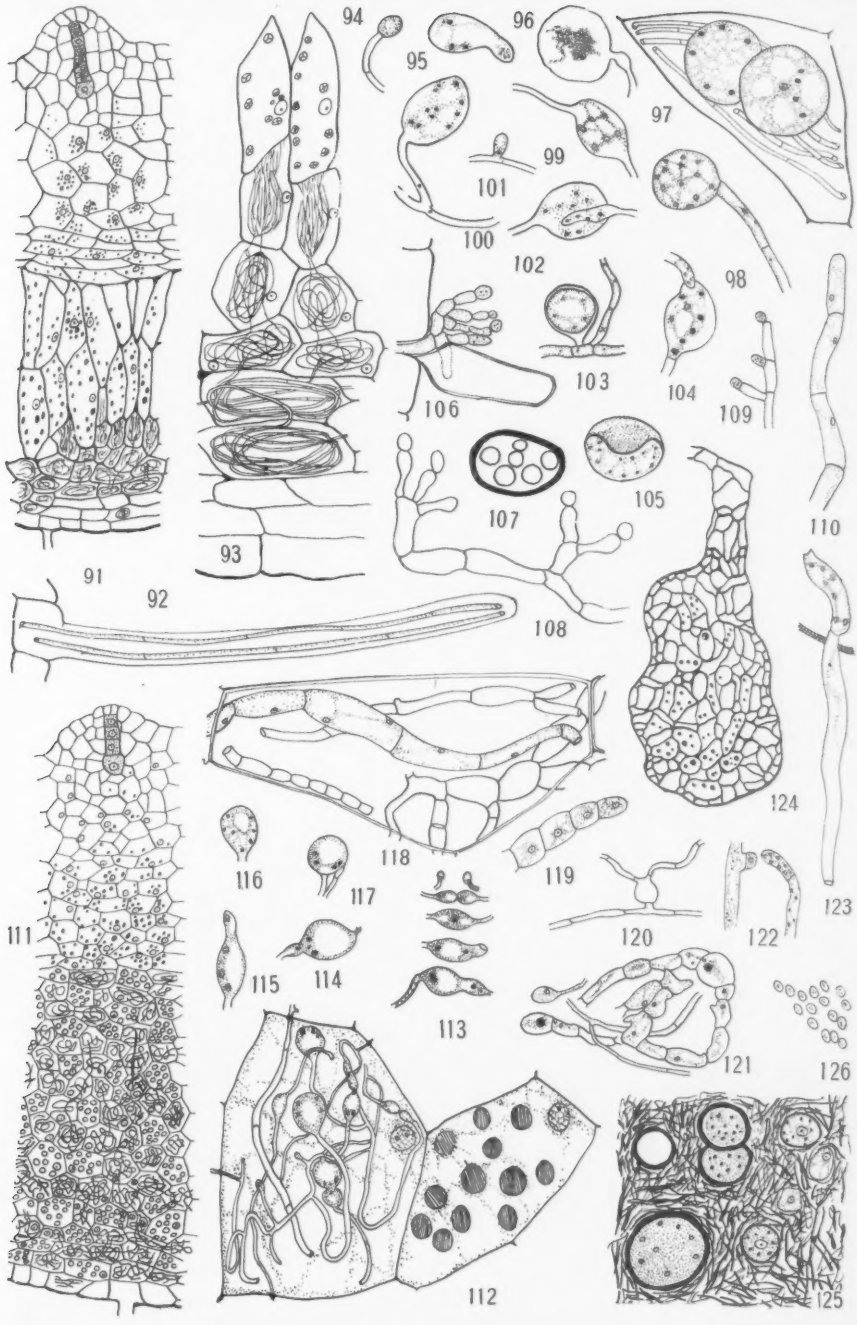


SPESSARD on LYCOPODIUM

PLATE XVII. PROTHALLIA OF L. obscurum

FIGS. 65–70.—Habit sketches of typical prothallia; ×2.

FIG. 71.—Sporeling growing from prothallium which grew in inverted position; natural size.

FIG. 72.—Germinating spore containing oil drops; ×775.

FIGS. 73–80.—Moderately young and mature prothallia in topographic view; ×10.

FIG. 81.—Antheridial mass enlarged, as seen when pressed out under cover glass; ×85.

FIG. 82.—Opercular cells of antheridium; ×375.

FIGS. 83–86.—Stages in development of archegonium; ×375.

FIGS. 87–89.—Stages in antheridial development; ×775.

FIG. 90.—Diagrammatic reconstruction of abnormal archegonial group, constructed from serial camera drawings.

PLATE XVIII. ENDOPHYTIC FUNGUS

(All figs. ×775 diameters, except figs. 91 and 111, which are × about 80.)

Endophytic fungus of *L. obscurum*

FIG. 91.—Distribution of fungus in prothallium.

FIG. 92.—Two mycelial threads within rhizoid.

FIG. 93.—Three special layers of cells containing the fungus; mycelial threads of upper layer applied closely to walls of starch-bearing cells; reproductive cells, when present, found only in two lower layers.

FIGS. 94–105.—Intracellular reproductive structures.

FIG. 106.—Branch of intercellular mycelium leaving prothallium at base of rhizoid.

FIG. 107.—Cross-section of a rhizoid containing six mycelial threads.

FIGS. 108–110.—Intercellular vegetative structures.

Endophytic fungus of *L. lucidulum*

FIG. 111.—Distribution of fungus in prothallium.

FIG. 112.—Two neighboring cells; one at left contains mycelial threads bearing reproductive structures, while other has no threads, but contains numerous spherical structures whose nature has not been determined.

FIGS. 113–117.—Various reproductive structures, intracellular.

FIGS. 118–123.—Vegetative structures, intercellular.

FIG. 124.—Ascomycetous-like structure found on epidermis of both species of prothallia, but connected with internal mycelium.

FIG. 125.—Degenerated prothallia cells, with reproductive structures.

FIG. 126.—Sporelike bodies found several times in mass of fig. 125; suggestive of ascospores.

NEW SOUTH AMERICAN ASTERACEAE COLLECTED BY E. W. D. HOLWAY

S. F. BLAKE

(WITH PLATE XIX)

The new species of Asteraceae here described form part of a collection made by E. W. D. HOLWAY and Mrs. MARY M. HOLWAY in Ecuador and Bolivia in 1920. A few have previously been found by other collectors, notably by J. N. ROSE, who visited a part of the same region in 1918. Although Professor HOLWAY'S interest is primarily in rusts rather than flowering plants, his appreciation of the value of precise identification of host plants has resulted in the preparation of complete and well dried specimens which have considerably increased our knowledge of the phanerogamic flora of the regions in which he has collected. Not the least valuable result of his work in Central and South America is the discovery of many new species of flowering plants, particularly Asteraceae, represented by specimens far superior to those of many collectors who confine their attention to phanerogams.

Achyrocline glandulosa, sp. nov.—Perhaps suffrutescent below, 40 cm. high and more, branched; branches ascending, simple, like the stem densely glandular-pubescent, winged throughout by the decurrent leaf bases, the wings herbaceous, 1–1.5 mm. wide; leaves lanceolate or linear-lanceolate, 3.5–6 cm. long, 3.5–7 mm. wide, acuminate, not narrowed at the long-decurrent base, entire, green on both sides, densely glandular-puberulous, arachnoid-ciliate, triplinerved; panicles rounded or flattish, 3–7 cm. wide, dense, the heads densely glomerate on the branchlets, the glomerules at base loosely pilose-tomentose like the branches of inflorescence; involucre oblong-cylindric, 4–4.5 mm. high, whitish or pale straw color, the phyllaries somewhat graduated, scarious, oblong or elliptic-ovate, obtuse, glabrous; ♀ flowers 4 or 5, ☿ 2; receptacle alveolate; ♀ corollas tubular-filiform, whitish, glabrous, 4-dentate, 3 mm. long, the style included; ☿ corollas slender, glabrous, 3 mm. long, 5-toothed, the throat slightly ampliate above; achenes oval, glabrous,

0.7 mm. long; pappus 3 mm. long, the slender bristles denticulate above, deciduous singly or in pairs.

ECUADOR.—Cuenca, September 10, 1920, *E. W. D.* and *M. M. Holway* 982 (type in U.S. National Herbarium no. 1058640).

Allied to *A. alata* (H. B. K.) DC., which has fuscescent phyllaries and leaves with long scattered hairs above. No reference is made in the description of that species to the glands which are so abundant in *A. glandulosa*, and which give it the fragrant odor of *Gnaphalium obtusifolium*.

Achyrocline hyperchlora, sp. nov.—Slender herb, 40 cm. high and more, branching, the base not seen; stem and branches flexuous, wingless, stipitate-glandular and scantily arachnoid-tomentose, glabrescent; leaves elliptic-lanceolate, 3–5.5 cm. long, 6–15 mm. wide, acuminate or acute, cuneate into a petioliform margined base decurrent for about 1 mm., entire, membranaceous, triplinerved, glandular on both sides, above green, pubescent with several-celled hairs, loosely arachnoid, glabrescent, beneath persistently griseous-arachnoid-pilose; panicles loose, much branched, leafy bracted, the heads in small glomerules, involved in wool at base; involucre 3 mm. high, whitish faintly tinged with straw color, the outermost phyllaries brownish toward base, the phyllaries oval to oblong, obtuse, scarious, stipitate-glandular and lanate-pilose toward base; ♀ flowers 4, ☿ 1; ♀ corollas whitish, tubular-filiform, stipitate-glandular at apex, 1.8 mm. long; ☿ corollas similar but thicker, 5-dentate; achenes immature; pappus 2 mm. long.

BOLIVIA.—Cochabamba, March 14, 1920, *E. W. D.* and *M. M. Holway* 406 (type in U.S. National Herbarium no. 1058598).

This species has the same sweet odor as *A. glandulosa*. It is of the *A. vargasiana* group, and is distinguished especially by the character of its leaves and its loose panicle.

Polymnia eurylepis, sp. nov.—"Slender tree 4–5 m. high"; branches stout, sulcate, densely hirsute-pilose with several-celled sordid hairs and somewhat glandular-puberulous, glabrescent; leaves opposite; petioles rather narrowly margined, densely pubescent like the stem, 1–3.5 cm. long; blades broadly ovate or rhombic-ovate, 7–19 cm. long, 4.5–11.5 cm. wide, acuminate, at base broadly cuneate, then gradually cuneate to the base of the petiole, remotely

denticulate (teeth minute, about 5 mm. apart), submembranaceous, above densely glandular-puberulous along the nerves, essentially glabrous on surface, beneath duller green, evenly but not densely hirsute-pilose, densely so along the veins and somewhat glandular there, triplinerved above the base and loosely prominulous-reticulate beneath, bullate in age above; heads 2 cm. wide, very numerous in panicles 9–19 cm. wide; bracts ovate, 6–15 mm. long; pedicels often decurved, glandular-puberulous and hirsute-pilose with several-celled hairs, 1–3.5 cm. long; disk subglobose, 6–8 mm. high, 8–13 mm. wide; outer phyllaries 5, broadly ovate, acutish, thin-herbaceous, ciliate, otherwise glabrous, 6–9 mm. long, 4.5–6 mm. wide; inner phyllaries (subtending the rays) oblong-oval, obtuse, membranous, hirsute-pilose, 6 mm. long; rays 12–14, yellow, exceeding the involucre, the lamina oval, 7 mm. long, 3.5 mm. wide, the tube densely hirsute-pilose; disk corollas yellow, sparsely hispid-pilose, 3.8 mm. long (tube 1.8 mm., throat broadly campanulate, 1.5 mm., teeth 0.5 mm.); pales acute, vittate, sparsely hirsute-pilose dorsally, 3.5 mm. long; ray achenes obliquely turbinate-subglobose, somewhat compressed, blackish, glabrous, 3 mm. long.

VENEZUELA.—Santo Domingo, altitude 2200 m., December 2, 1910, *Alfredo Jahn* 128.

ECUADOR.—Along fences, Cuenca, September 10, 1920, *E. W. D.* and *M. M. Holway* 974 (type in U.S. National Herbarium no. 1058639); Ficoa, near Ambato, February 1919, *A. Pachano* 135.

This species is related to *P. lehmannii* Hieron., which has broadly margined petioles, merely glandular-puberulous pedicels, smaller outer phyllaries (5.5 by 1.75 mm.), which are puberulous at base, and 7–10 rays. It is also near *P. arborea* Hieron., but in that species, represented in the National Herbarium by fragments from the type, the somewhat larger outer phyllaries are densely stipulate-glandular and sparsely hirsute-pilose on the back. HOLWAY's label gives the height of the plant as 12–15 ft. PACHANO calls it a "slender tree," and gives the vernacular name as "polaco"; JAHN gives the name "aníme."

Monopholis, gen. nov.—Shrubs with large alternate serrulate or subentire leaves and many-headed terminal panicles of small pale yellow cylindric heads; heads homogamous or heterogamous, the disk flowers hermaphrodite, fertile, those of the ray when present pistillate; involucre about 3-seriate, graduate, passing into the pales, the phyllaries chiefly linear-elliptic or elliptic, indurated-

subherbaceous, appressed; receptacle small, convex; pales firm, subindurate, persistent, all or the inner with thinner inflexed margins, more or less completely inclosing the achenes; ray corollas usually none, when present solitary, ligulate, fertile, the lamina oval, bidenticulate to trifid; disk corollas with slender tube, short broadly campanulate throat, and 5 equal or longer reflexed teeth; stamens with minutely sagittate base and ovate terminal appendages; style branches rather short, slightly recurved, with deltoid obtuse papillose-hirsutulous tips; achenes linear-fusiform, narrowed to the callous base, often shortly subrostrate, more or less compressed, lenticular or trigonous in cross-section, wingless, glabrous; pappus of a single usually broad deltoid to rhombic-lanceolate or oblong paleaceous persistent awn borne on the inner side of the achene, or rarely wanting.—Type species *M. hexantha* Blake.

A genus of four closely related species from the mountains of Ecuador and Peru, related on the one hand to *Verbesina*, on the other to the imperfectly known *Monactis* H. B. K. In habit and many other characters it makes a rather close approach to the Andean species of the section LIPACTINIA of *Verbesina*, but differs greatly in its linear-fusiform subrostrate wingless achene with a pappus of a single broad paleaceous awn. Its relationship to *Monactis* is closer, but the same characters of achene and pappus suffice to distinguish it. The short, broadly campanulate corolla throat equaled or exceeded by the spreading or reflexed teeth is also characteristic of *Monopholis*. The genus may be inserted in the system next to *Monactis*.

In addition to the two species here described as new, two species described by HIERONYMUS under *Chaenocephalus* but referable to this genus are represented by fragments in the National Herbarium. The following key will serve to separate the species.

Heads chiefly pedicellate, the pedicels 1–7 mm. long.

Heads 6 or 7-flowered, 6–8 mm. high (excluding the corollas), 1.5–3 mm. thick in fruit; involucre 3.5–4.5 mm. high; broader phyllaries 1–1.5 mm. wide..... 1. *M. hexantha*

Heads about 12-flowered, 7–9 mm. high (excluding the corollas), 3–4 mm. thick in fruit; involucre 5–6 mm. high; broader phyllaries 1.8 to 2 mm. wide..... 2. *M. pallatangensis*

Heads chiefly sessile, rarely short-pedicellate.

Branches loosely sordid-puberulous; leaves broadly ovate; ☿ flowers 8–11, ♀ 0; pappus awn 1.3–1.5 mm. long..... 3. *M. holwayae*

Branches "densely velvety-pubescent"; leaves lance-ovate or lanceolate; ☿ flowers 7 or 8, ♀ 1 or 0; pappus awn 0.4–0.8 mm. long 4. *M. jelskii*

1. **Monopholis hexantha,** sp. nov.—Shrub (or tree?); branches flexuous, striate-angulate, 4 mm. thick, obscurely griseous-puberulous with matted hairs; branchlets of the year fuscous, sordid-puberulous with loose several-celled subglandular hairs; internodes 1–2 cm. long; leaves alternate, often with fascicles of reduced leaves in their axils; petioles slender, naked, puberulous, 7–13 mm. long; blades lance-ovate or the smaller lanceolate, 6–12 cm. long or more, 1.8–5.5 cm. wide, acuminate, at base acutely cuneate into the petiole, serrulate (teeth depressed, less than 1 mm. high, 2–4 mm. apart) or the smaller entire or subentire, pergamentaceous, above green, harshly tuberculate-hispidulous with mostly deciduous hairs, beneath densely and softly griseous-tomentose-pilosulous with crisped hairs and gland-dotted, triplinerved above the base, bullate-rugulose above, prominulous-reticulate beneath; panicles terminating the branchlets, many-headed, flattish or rounded, 9–13 cm. wide, sordid-puberulous, the lower branches subtended by reduced leaves, the upper bracts linear, minute; pedicels 5 mm. long or usually less, often suppressed; heads discoid, 6 or 7-flowered, cylindric, 6–8 mm. high, 1.5–3 mm. thick; involucre graduate, about 3-seriate, 3.5–4.5 mm. high, passing gradually into the receptacular pales, the phyllaries linear-oblong to elliptic or sometimes elliptic-obovate, obtuse or rounded, subherbaceous-indurated, greenish-white, sordid-ciliate, somewhat glandular-puberulous, the outermost with narrow thinner sometimes purplish-tinged margins; corollas apparently pale yellow, the tube sparsely pilose with several-celled hairs, 1.8 mm. long, the throat broadly campanulate, glabrous, 0.8–1 mm. long, the 5 teeth lance-ovate, acute, spreading or reflexed, glabrous, 1 mm. long; pales linear-elliptic, obtuse, somewhat puberulous and ciliolate, about 5 mm. long, similar to the inner phyllaries but longer, their margins somewhat thinner, inflexed and inclosing the achenes, triangular or rhombic in cross-section; achenes linear-fusiform, 3.5–4.5 mm. long, 0.6 mm. wide, lenticular or trigonous in cross-section, shortly subrostrate, blackish-brown, with callous whitish carpopod, glabrous, finely papillose; pappus awn rhombic-lanceolate or oblong, flat, acute or obtuse, usually sparsely denticulate, 1.2–1.6 mm. long, about 0.3 mm. wide.

ECUADOR.—Cuenca, September 10, 1920, *E. W. D.* and *M. M. Holway* 973 (type in U.S. National Herbarium no. 1058646).

2. **Monopholis pallatangensis** (Hieron.) Blake.—*Chaenocephalus pallatangensis* Hieron. Bot. Jahrb. Engler **29**:47. 1900.

Known only from the type collection made by SODIRO (no. 38) in the Pallatanga Valley, Ecuador. Fragments are in the U.S. National Herbarium. HIERONYMUS describes the heads as 9 or 10-flowered, but I have found 12 flowers (all tubular) in each of two heads dissected.

3. **Monopholis holwayae,** sp. nov.—Branches stoutish, flexuous, striate-ridged, sordid-puberulous with crisped hairs; internodes 2–5.5 cm. long; leaves alternate; petioles pubescent like the stem, naked, 7–15 mm. long; blades ovate, 8–18 cm. long, 3–8 cm. wide, acuminate, acutely cuneate into the petiole, remotely crenulate-serrulate and somewhat repand or subentire, pergamentaceous, above deep green, densely and harshly tuberculate-hispidulous, along the veins sordid-puberulous, bullate in age, beneath rather densely and softly griseous-pilosulous-tomentose and gland-dotted, sordid-pilosulous along the chief veins, triplinerved above the base, prominulous-reticulate beneath; panicles terminating the branchlets, flattish or convex, many-headed, 8–10.5 cm. wide, sordid-puberulous with crisped subglandular hairs; pedicels usually obsolete, sometimes up to 2 mm. long; heads discoid, 8 to 11-flowered, cylindric, 9–10 mm. high, 2.5–3.5 mm. thick; involucre graduate, about 3-seriate, 4–5 mm. high, the phyllaries linear-elliptic or the inner oblong, obtuse, subindurate below and with thinner hyaline-subherbaceous greenish-yellow tip, sordid-ciliate, sparsely glandular, passing into the pales of disk; corollas apparently pale yellow, the tube sparsely long-pilose with several-celled hairs, 2 mm. long, the broadly campanulate glabrous throat 1 mm. long, the lance-ovate acute reflexed glabrous teeth 1.5 mm. long; pales elliptic, obtuse, sordid-ciliate, dorsally sordid-pilose and somewhat glandular, about 7 mm. long, the inner with inflexed margins more or less closely enveloping the achenes, the outer flattish; achenes similar to those of *M. hexantha* but with more acutely tapering base, 4.5 mm. long; pappus awn 1.3–1.5 mm. long.

ECUADOR.—Cuenca, September 15, 1920, *E. W. D.* and *M. M. Holway* 989 (type in U.S. National Herbarium no. 1058649).

The species is named in compliment to Mrs. MARY M. HOLWAY, who accompanied Professor HOLWAY on his South American trip.

4. **Monopholis jelskii** (Hieron.) Blake.—*Chaenocephalus jelskii* Hieron. Bot. Jahrb. Engler **36**:494. 1905.

Known only from the type collection by JELSKI (no. 698), made near Tambillo, Peru, August 10, 1878. Fragments are in the U.S. National Herbarium. The pappus awn is rarely wanting in some of the flowers of a head, as noted by HIERONYMUS, but I have seen no case in which there was a second shorter awn, such as he describes, present in the pappus. This appearance may have been due to a splitting of the awn into two, the possibility of which is indicated by the occasional occurrence of a deeply emarginate or bifid awn in this or other species.

Wedelia holwayi, sp. nov.—Shrub, trichotomously branched; branches slender, hispidulous and hispid hirsute with tuberculate-based spreading or reflexed hairs 1 mm. long or less; leaves opposite; petioles hirsute, 1–3 mm. long; blades lance-ovate, 3.5–6 cm. long, 1–2 cm. wide, acuminate, cuneate at base, remotely serrulate (teeth 4–10 pairs, 3–7 mm. apart), papery, above very harshly tuberculate-hispidulous and tuberculate-hirsute, beneath equally green, hirsutulous and hirsute, triplinerved, prominulous-reticulate beneath; heads in threes at apex of stem and branches, 2–3 cm. wide, on densely hispidulous and hirsute naked or 1-bracteate peduncles 2–6 cm. long; disk 1–1.3 cm. high, 1.3–1.6 cm. thick; involucre 3 or 4-seriate, graduate, 1–1.2 cm. high, the outermost phyllaries obovate-oblong, herbaceous throughout or indurated at base, acutish to obtuse, ciliate, tuberculate-glandular and sparsely tuberculate-hirsute, 5–8 mm. long, 3–4 mm. wide, the innermost elliptic-oblong or oblong with membranous-herbaceous ciliate rounded tip, on back essentially glabrous, the middle series intermediate in characters, all erect or with loose tips; rays about 12, golden yellow, fertile, the lamina elliptic, 8–14 mm. long, 3–4 mm. wide; disk corollas yellow, hispidulous toward base of throat, 6.5–7 mm. long (tube 2–2.5 mm.), the teeth papillose-hispidulous on margin within; pales subscarious, obtuse or acute, spinulose-denticulate above, 7–8 mm. long; ray achenes bluntly trigonous, not winged or auriculate, sparsely pilose, their pappus cyathiform, fimbriatulate, 0.8 mm. long, with a partly free awn 1 mm. long on the inner angle; disk achenes narrowly obovoid, thickened, densely pilose, wingless, without ears above, 3.8 mm. long, their pappus cyathiform, narrow, 1 mm. high, lacerate-fimbriate, with 1 awn 1.5 mm. long.

BOLIVIA.—Cochabamba, March 7, 1920, *E. W. D.* and *M. M. Holway* 376 (type in U.S. National Herbarium no. 1058597).

Nearest the Peruvian *W. forbesii* S. Moore, which has smaller lanceolate leaves, longer peduncles, and shorter involucre and rays.

Wedelia isolepis, sp. nov.—Apparently suffrutescent, dichotomously or trichotomously branched; stem and branches terete, evenly but not densely spreading-hirsute with scarcely tuberculate-based hairs 1 mm. long or less and somewhat puberulous, glabrate or glabrescent; internodes 8–16 cm. long; leaves opposite; petioles hirsute, 1.5–5 mm. long; blades ovate, 5–8 cm. long, 2.5–3.8 cm. wide, acute or acuminate, at base cuneate-rounded, remotely crenate-serrate or crenate-serrulate (teeth depressed, 3–8 mm. apart), papery, above deep green, harshly hispidulous and hirsute (the larger hairs with persistent lepidote-tuberculate bases), beneath paler green, evenly but not densely hirsutulous and along the veins spreading-hirsute, triplinerved above the base, prominulous-reticulate beneath; heads in threes at apex of stem and branches, 3.5–4 cm. wide, on naked densely hirsutulous and hirsute monocephalous peduncles 1.8–9 cm. long; disk 1–1.2 cm. high, 1.5–1.8 cm. wide; involucre 3-seriate, 10–11 mm. high, equal or the innermost series sometimes shorter, the two outer series of phyllaries equal, oval, herbaceous throughout or somewhat indurated at base, obtuse, rounded, or sometimes acutish, hirsute and minutely hirsutulous, the innermost equal or shorter, with ciliate, purplish, membranaceous tips, dorsally glabrous, all often reflexed at tip; rays 12, golden yellow, fertile, the lamina oval, tridentate, 15 mm. long, 7 mm. wide; disk corollas yellow, papillose-hispidulous on teeth, 6.5 mm. long (tube 2 mm.); pales acute, carinate, glabrous, yellowish and spinulose-denticulate above, about 5 mm. long; disk achenes obovoid, thickened, mottled, sparsely pilose, 3 mm. long; pappus cyathiform, 0.5 mm. high, fimbriolate.

BOLIVIA.—Soratá, April 14, 1920, *E. W. D.* and *M. M. Holway* 517 (type in U.S. National Herbarium no. 1058604).

Well distinguished by its involucral characters.

Helianthus hypargyreus, sp. nov.—Evidently tall, herbaceous at least above; stem stout, pithy, subterete, densely and softly cinereous-pilosulous with reflexed or spreading hairs, glabrescent or glabrate; internodes 2–13 cm. long; leaves alternate; petioles

naked or margined above, those of the stem leaves 1–5 cm. long, densely cinereous-pilosulous; stem leaves ovate or broadly ovate, 6–15 cm. long, 3–8.5 cm. wide, acuminate, at base broadly rounded, then shortly cuneate into the petiole, crenate-serrate above the entire base (teeth 12–18 pairs, depressed-triangular, obtuse, 1–2 mm. high, 2–5 mm. apart), thin-papery, above dull greenish, densely and softly cinerescent-pilosulous with ascending hairs with small tuberculate-subglandular bases, beneath very densely and softly argenteous-pilose (sometimes yellowish-tinged) with subappressed lucid hairs, triplinerved just above the base, the primary veins evident beneath, the secondaries mostly concealed by the pubescence; branch leaves smaller, sometimes subentire; heads 2–3 cm. wide, in corymbose panicles of 3–9 at tips of branches and branchlets, the pedicels 1–5.5 cm. long, densely tomentulose-pilosulous; disk depressed-subglobose, 8 to (fruit) 14 mm. high, 1.2 to (fruit) 1.8 cm. wide; involucre 3-seriate, graduate, 9–15 mm. high, the phyllaries lanceolate or lance-elliptic to oblong-lanceolate, with indurate vittate base and shorter or equal to (outermost) longer reflexed or spreading acute herbaceous tips, densely sericeous- or cinereous-pilose-tomentose outside above the sparsely pubescent indurated base, the herbaceous apex densely pilosulous; receptacle slightly convex; rays 12, golden yellow, neutral, the lamina hirsutulous dorsally, elliptic-oblong or oval, 2 or 3-denticulate, 7–13 mm. long, 3–5.5 mm. wide; disk corollas yellow, hirsutulous chiefly at base of throat and on teeth, 5.5 mm. long (tube 1.6 mm., teeth 0.8 mm.); pales acute, carinate, hirsutulous at apex and very sparsely along keel, about 8 mm. long; achenes oblong-obovate, strongly compressed, blackish, glabrous, 2.5–3 mm. long, 1.2 mm. wide; awns 2, subequal, deciduous, narrowly lance-subulate, hispidulous throughout, 2.5 mm. long; squamellae none.

ECUADOR.—Huigra, Province of Chimborazo, August 3, 1920, *E. W. D.* and *M. M. Holway* 815 (type in U.S. National Herbarium no. 1058651); same locality, August 18 and September 6, 1918, *J. N.* and *G. Rose* 22171 and 22568.

This rather handsome species is related to *H. imbaburensis* and *H. lehmannii* Hieron., both of which are now represented in the U.S. National Herbarium by fragments from the types. The former differs in its narrower entire leaves and much smaller heads, the latter in its black-purple disk and longer, acuminate phyllaries.

Perymenium ecuadoricum, sp. nov.—Shrub(?); stem (above) and branches herbaceous, 4 mm. thick, harshly spreading- or ascending-hispidulous, or sometimes strigillose; leaves opposite; petioles naked, 7–20 mm. long, tuberculate-strigillose, hirsute-ciliate; blades ovate, 5–10.5 cm. long, 2.5–5 cm. wide, acuminate or acute, at base truncate-rounded or rounded to cordate, crenate-serrulate throughout (teeth about 32 pairs, obtuse, about 1 mm. high), thick-papery, above deep green, bullate-rugulose, harshly tuberculate-hispidulous, beneath densely and almost softly griseous-hirsutulous-pilosulous and along the veins hirsute, triplinerved, the veins and veinlets impressed above, densely prominulous-reticulate beneath; peduncles ternately arranged, terminal and from the upper axils, strigillose or erect-hirsutulous, 3.5–9.5 cm. long, bearing 2–4 heads on pedicels 1–5 cm. long, the bracts mostly very small, rarely leaflike; heads 2.5–3 cm. wide; disk subglobose, 7–8 mm. high, 8–10 mm. thick; involucre 4-seriate, graduate, 7–8 mm. high, the phyllaries broadly oval or the outermost oblong-ovate, with somewhat indurated base and shorter or subequal herbaceous or membranous-herbaceous rounded appressed tip, strigillose and ciliate, the inner glabrous above on back; rays 12, golden yellow, fertile, the lamina oblong-elliptic, 13 mm. long, 4.5 mm. wide; disk corollas yellow, papillose-hispidulous on teeth, 4.8 mm. long; pales obtuse to acute, minutely spinulose-denticulate on keel and toward apex, about 4 mm. long; disk achenes oblong, 2 mm. long, somewhat thickened but compressed, transversely rugulose, sparsely hispidulous above, often narrowly winged above on the inner side and there produced into an ear about 0.5 mm. high, sometimes also with a shorter tooth on the outer angle; pappus fragile, of about 10 unequal slender hispidulous awns 0.8 mm. long or less, and 1 awn twice as long.

ECUADOR.—Huigra, Province of Chimborazo, August 3, 1920, *E. W. D.* and *M. M. Holway* 828 (type in U.S. National Herbarium no. 1058652); same locality, August 18, 1918, *J. N.* and *G. Rose* 23820.

Closely related to the Peruvian *P. jelskii* (Hieron.) Blake (*Wedelia jelskii* Hieron. Bot. Jahrb. Engler **36**:488. 1905), of the type of which ample fragments are now in the National Herbarium. In that species, however, the leaves beneath are pale green rather than griseous, and much less densely pubescent, and their petioles are only 4–7 mm. long, while the stem is rather sparsely strigillose.

Steiractinia rosei, sp. nov.—Shrub; stem stout, densely sordid-pilose with matted erectish or loose hairs with small tuberculate bases, glabrescent; leaves opposite; petioles pubescent like the stem, naked, 7–17 mm. long; blades ovate or the smaller lance-ovate, 8–14 cm. long, 3.5–7 cm. wide, acuminate, at base cuneate-rounded, closely crenate-serrate or crenate-serrulate with depressed teeth, papery, above green, densely and harshly tuberculate-hispidulous, along the chief veins sometimes densely pilose, beneath rather softly and densely griseous-pilosulous or short-pilose, triplinerved above the base, impressed-veined and somewhat bullate above, prominulous-reticulate beneath; peduncles in threes at tip of stem and branches, pubescent like the stem, 3–8 cm. long, bearing 1 or sometimes 2 or 3 heads, usually naked; heads about 4 cm. wide; disk depressed-subglobose, in flower 8–12 mm. high, 8–15 mm. thick, in fruit 1.2–1.5 cm. high, 1.5–2 cm. thick; involucre about 4-seriate, graduate, 9 to (fruit) 15 mm. high, the outermost phyllaries suborbicular, herbaceous or with indurated base, acute or apiculate to obtuse, strigillose and somewhat strigose, 7–9 mm. long, 5–7 mm. wide, the middle ones very broadly obovate-oval, with rounded ampliate submembranous loose upper portion, ciliate, on back somewhat strigose or hirsute and strigillose, 8–11 mm. wide, the innermost similar but smaller and shorter, often nearly glabrous; rays 10, neutral, yellow, the lamina elliptic-oblong, when well developed 2.5 cm. long, 8 mm. wide; disk corollas yellow, 5.8 to (in age) 7.8 mm. long (tube 1.5–2.8 mm., throat 3.5–4.2 mm., teeth sparsely hispidulous near tip, papillose along margin within, 0.8 mm. long); pales narrow, acute, carinate, spinulose-denticulate above, about 8 mm. long; achenes obovate-oblong, compressed, blackish, narrowly 2-winged, 3.8 mm. long, sparsely hirsute-pilose, on the wings hirsute-ciliate, slightly contracted at apex into a collar about 0.3 mm. high, this bearing the caducous pappus of about 30 slender unequal hispidulous awns 3 mm. long or less.

ECUADOR.—Huigra, Province of Chimborazo, August 4, 1920, *E. W. D.* and *M. M. Holway* 832. Vicinity of Loja, September 29–October 3, 1918, *J. N. Rose, A. Pachano,* and *G. Rose* 23290 (type in U.S. National Herbarium no. 1023389).

Related to *S. sodiroi* (Hieron.) Blake, which has larger heads and outer phyllaries rather abruptly contracted into an indurated base.

Verbesina adenobasis, sp. nov.—Shrubby (?); branches stout, herbaceous, pithy, sordid-pilosulous with crisped hairs, glabrescent; leaves opposite or subopposite; petioles sordid-pilosulous, marginate above, stout, 1–2.5 cm. long; blades broadly ovate or rhombic-ovate, 12–17 cm. long, 7–10 cm. wide, sometimes with a short triangular lobe on one side near middle, acute, at base rounded-cuneate, then cuneately decurrent on the upper part of the petiole, serrulate above the base (teeth about 40 pairs, slender, acutish, 1 mm. high), papery-pergamentaceous, above deep green, densely scabrid-hispidulous with glandular-tuberculate-based hairs, very densely so along the veins, beneath rather densely hirsutulous-pilosulous with crisped somewhat deciduous sordid hairs (those along the veins dense and brownish), triplinerved above the base, loosely prominulous-reticulate beneath; panicle terminal, ternately divided, very many-headed, flattish, about 22 cm. wide, densely sordid-pilosulous with several-celled crisped sordid subglandular hairs; bracts minute; pedicels 3–14 mm. long, sometimes obsolete, naked or with minute bractlets; heads narrowly becoming broadly campanulate, the disk 8–11 mm. high, 3–4.5 mm. thick; involucre about 3-seriate, graduate, about 4 mm. high, passing into the pales, the outermost phyllaries small, linear-oblong or spatulate-oblong, herbaceous, obtuse or rounded, glandular-puberulous, ciliolate, 1.5–2 mm. long, 1 mm. wide or less, the inner oblong, obtuse, 1–1.3 mm. wide, ciliolate, otherwise glabrous, greenish-white, all appressed; rays 2 or 3, pale yellow, fertile, the lamina oval, 4.5 mm. long, 2.8 mm. wide; disk flowers 11 or 12, their corollas pale yellow, pilose on tube with several-celled hairs, 5.5–6 mm. long (tube 1.5–2 mm., throat cylindric-funnelform); pales obtuse, glabrous or somewhat ciliolate, 6 mm. long; ray achenes trigonous, 3-awned; disk achenes obovate, very flat, essentially glabrous, 5 mm. long, the body 1.5 mm. wide, 2-winged, the wings 0.5–0.9 mm. wide; awns 2, subequal, subterete, sparsely hispidulous, 3.5–4 mm. long.

ECUADOR.—In shrubbery along roads, Cuenca, September 15, 1920, *E. W. D.* and *M. M. Holway* 991 (type in U.S. National Herbarium no. 1058641).

A member of the *V. arborea* group, related to *V. lloensis* Hieron., which has velvety-tomentose branches, oblong alternate leaves, 3–6 ray flowers or none, and 12–18 disk flowers.

Verbesina latisquama, sp. nov.—Shrub (?); branch stout, herbaceous, pithy, striate-subangulate, sordid-pilosulous with crisped hairs, glabrescent; leaves opposite; petioles stout, densely sordid-pilosulous, marginate above, the naked part 7–13 mm. long; blades ovate, 10–16 cm. long, 4.5–8.5 cm. wide, sometimes with a short obscure lobe on one or both sides near middle, acuminate, at base cuneate-rounded and decurrent into the petiole, serrulate (teeth about 40 pairs, depressed, apiculate, 0.5 mm. high), papery, above deep dull green, densely scabrid-hirsutulous (the hairs with lepidote-tuberculate not glandular bases) and along the veins very densely sordid-hirsutulous, beneath rather densely subtomentose-pilosulous with griseous matted hairs (probably finally deciduous) and along the veins densely sordid-pilosulous, triplinerved above the base; panicle terminal, ternately divided, pubescent like the stem, very many-headed, flattish, about 18 cm. wide; bracts small; pedicels 4–10 mm. long, or obsolete; heads narrowly campanulate, the disk 9–10 mm. high, 4–5 mm. thick; involucre 2 to 3-seriate, graduate, 4–5 mm. high, the outermost phyllaries oblong or obovate-oblong, 2–3 mm. long, 1.2–1.5 mm. wide, with subindurate base and subequal rounded herbaceous tip, ciliolate, somewhat glandular and puberulous, the inner similar but oval-oblong, thinner, 2 mm. wide; rays 2 or 3, pale yellow, fertile, the lamina oval, 6–7 mm. long, 3.5 mm. wide; disk flowers 8–12, yellow, pilose on tube with several-celled hairs, 6 mm. long; pales minutely apiculate from a rounded ciliate apex, sparsely pilosulous on back, about 6 mm. long; achenes (very immature) glabrous; awns subequal, hispidulous above, about 4.5 mm. long.

ECUADOR.—In shrubbery along roads, Cuenca, September 15, 1920, *E. W. D.* and *M. M. Holway* 994A (type in U.S. National Herbarium no. 1058643).

Allied to *V. adenobasis* described above, but with different pubescence and toothing of leaves, larger rays, and much broader phyllaries.

Calea huigrensis, sp. nov.—Shrub 1–3 m. high; stem terete, densely hispidulous-puberulous and hirsute-pilose with several-celled spreading hairs, the long ones mostly deciduous or sometimes entirely wanting; leaves opposite; petioles hispidulous-puberulous and gland-dotted, corky-thickened at base, 4–7 mm. long; blades

ovate, those of the main stem 4–7.5 cm. long, 2–3.8 cm. wide, acute, at base rounded or cuneate-rounded, serrulate (teeth small, 4–7 pairs), slightly revolute-margined, papery, harshly tuberculate-hispidulous above, beneath equally green, densely gland-dotted, hispidulous along the veins, 3-nerved and prominent-reticulate, above impressed-veined and rugose; heads in umbelliform clusters of 5–9 at tips of stem and branchlets, on densely puberulous pedicels 3–12 mm. long, 21-flowered, campanulate, 9–10 mm. high, 4–6 mm. thick; involucre 6–7 mm. high, about 5-seriate, graduate, the outermost phyllaries ovate, 1.5 mm. long, with callous tip, puberulous and gland-dotted, the middle phyllaries oblong, rounded, brownish above, subscarious, vittate, sometimes ciliolate, obscurely puberulous above or glabrous, the inner obovate-oblong or oblong, rounded, vittate, yellow, scarious, glabrous, all appressed; rays 3, fertile, golden yellow, erectish, the lamina oblong, 3 mm. long; disk flowers 18, their corollas golden yellow, glabrous, 6 mm. long (tube 2.2 mm., throat cylindric, 3.2 mm., teeth 0.6 mm.); pales yellow, scarious, acute, obtuse, or bifid, glabrous, lacerate toward tip, 4.5 mm. long; achenes of ray and disk similar, hispidulous, 2.5 mm. long; pappus of 20 linear-lanceolate acuminate paleaceous awns 5 mm. long.

ECUADOR.—Banks of old railway grade, Huigra, Province of Chimborazo, August 7, 1920, *E. W. D.* and *M. M. Holway* 856 (type in U.S. National Herbarium no. 1058628); same locality, altitude 1525–1675 m., August 21, 1918, *J. N.* and *G. Rose* 22283.

A member of the section EUCALEA, related to *C. umbellulata* Hochr., which has glabrous achenes and only 6–9 disk flowers. The heads of this species impart a strong saffron color to the water in which they are boiled.

Gynoxys hypomalaca, sp. nov.—Shrub 3 m. high; stem stout, subterete, cinerous-tomentulose; young branches angled, densely cinereous- or ochraceous-tomentose; leaves opposite; petioles closely ochraceous-tomentose, 1.5–2.7 cm. long; blades ovate or oblong-ovate, 7–12 cm. long, 2.8–4.5 cm. wide, acuminate, apiculate, at base broadly rounded, obscurely and remotely serrulate with inflexed glandular teeth, appearing entire, coriaceous, above deep green, sparsely pilosulous, quickly glabrate except along the puberulous costa and sometimes the veins, beneath densely and softly

griseous- or ochraceous-tomentose with rather loose crisped hairs, feather-veined, the lateral veins about 10 pairs, plane or impressed above, prominent beneath, the veinlets finely prominulous-reticulate above, loosely prominulous-reticulate beneath; panicles terminal, many-headed, 9–12 cm. wide, ochroleucous-tomentose, the linear-spatulate or linear tomentose bracts 1 cm. long or less; pedicels 5 mm. long or less; heads 11–14 mm. wide; disk 1 cm. high, 8 mm. thick; involucre 7 mm. high, bearing at base 3 or 4 linear bractlets about 4 mm. long, the phyllaries 8, densely ochraceous-tomentose on their exposed surface, oval-oblong, obtuse; rays 7, yellow, the lamina 6 mm. long; disk flowers 16–18, their corollas yellow, 7.5 mm. long, glabrous, the teeth papillose at tip; achenes (immature) glabrous; pappus bristles spinulose throughout, dilated at tip, 6 mm. long.

BOLIVIA.—Higher limit of trees, Soratá, April 22, 1920, *E. W. D.* and *M. M. Holway* 567 (type in U.S. National Herbarium no. 1058605).

This seems to be distinct from any of the very numerous species which have been described within recent years. Its closest ally is apparently *G. caracensis* Muschler, which, according to description, has leaves with appressed fulvescent-cinereous tomentum beneath, 8–10 ♀ and 11–14 ☿ flowers, and a somewhat different involucre. *G. hypomalaca* comes from the same locality where MANDON collected so many new species, but of the two new species properly belonging to the genus, briefly described by SCHULTZ BIPONTIUS from his collections, one, *G. mandonii*, is of a different group, while the other, *G. asterotricha*, agrees in most of the few characters given with *G. hypomalaca*, but is said to have cordate leaves.

Mutisia sagittifolia, sp. nov.—Stem slender, supported among shrubs, essentially terete, obsoletely winged in places, about 2 mm. thick, at first densely white-arachnoid-tomentose, soon glabrate and brown; internodes 6–30 mm. long; leaves alternate, terminated by a simple cirrhus 1–3 cm. long, the blades linear or linear-lanceolate, 6–8 cm. long, 5–8 mm. wide, usually falcate, acute and unequal at apex, sessile and sagittate-auriculate at base (the acute ears 3 mm. long), coriaceous, entire, revolute-margined, 1-nerved, above quickly glabrous, shining green, impressed-venulose, beneath densely and persistently white- or cinereous-arachnoid-tomentose; peduncles solitary at tips of branches, 2 cm. long, apparently decurved, bearing a single small bract, tomentose like the stem;

rays erect, the head 7.5 cm. high, about 5 cm. wide; involucre strongly graduate, about 7-seriate, 4.8 cm. high, funnelform-campanulate, the three outer series of phyllaries with deltoid or broadly ovate body and subequal or longer, abrupt, linear or linear-lanceolate, erect, herbaceous tip (the latter 8–12 mm. long, 1 mm. wide), glabrous, the body blackish-green, with thin slightly wine-colored margins; those of the 4 inner series oval or oblong-oval, at the broadly rounded apex apiculate and arachnoid-tufted, otherwise glabrous, the inner thin and wine-colored throughout, the outer similar to the three outer series in texture and color; pistillate flowers 13, glabrous, the corollas erect, the tube 2.2 cm. long, the outer lip elliptic, 4 cm. long, 1 cm. wide, acutely 3-toothed, apparently yellow inside and dark (reddish?) outside, about 14-nerved, the inner lip of two narrowly subulate segments 7 mm. long; disk corollas numerous, apparently yellow tinged with reddish, bilabiate, glabrous, 3.5 cm. long, the throat fenestrate below on both sides, the lips subequal, about 13 mm. long, one 3-denticulate at apex, the other 2-parted to base; achenes glabrous, those of the ray obcompressed, 4 mm. long, glabrous, their pappus of easily deciduous plumose setae 2.5 cm. long; achenes of the disk similar, the pappus of about 26 plumose setae united at extreme base; ray flowers with imperfect anthers and glabrous style branches about 0.6 mm. long; auricles of the stamens of the disk 5 mm. long, acuminate, somewhat denticulate toward apex.

ECUADOR.—On slopes of Mt. Pichincha, August 23, 1920, *E. W. D.* and *M. M. Holway* 941 (type in U.S. National Herbarium no. 1058634).

Allied to *M. mathewsii* Hook and Arn. in its sagittate-based leaves, but in that species the leaves are only 1.5 mm. wide, and the involucre only 3–3.5 cm. long. Only a single plant of the new species was found.

Hieracium pazense, sp. nov.—Perennial, with 2 or more stems, about 45 cm. high, the root not seen; stems rather stout, branched from the middle, rather densely hispid-pilose to middle with spreading or reflexed whitish hairs about 4 mm. long, with blackish tuberculate bases, above the middle hispid-pilose with wide-spreading blackish hairs 2–7 mm. long, with subulate bases, the shorter ones often tipped with blackish glands, and also not densely glandular-puberulous; stem leaves (below the inflorescence) about 5, the lower

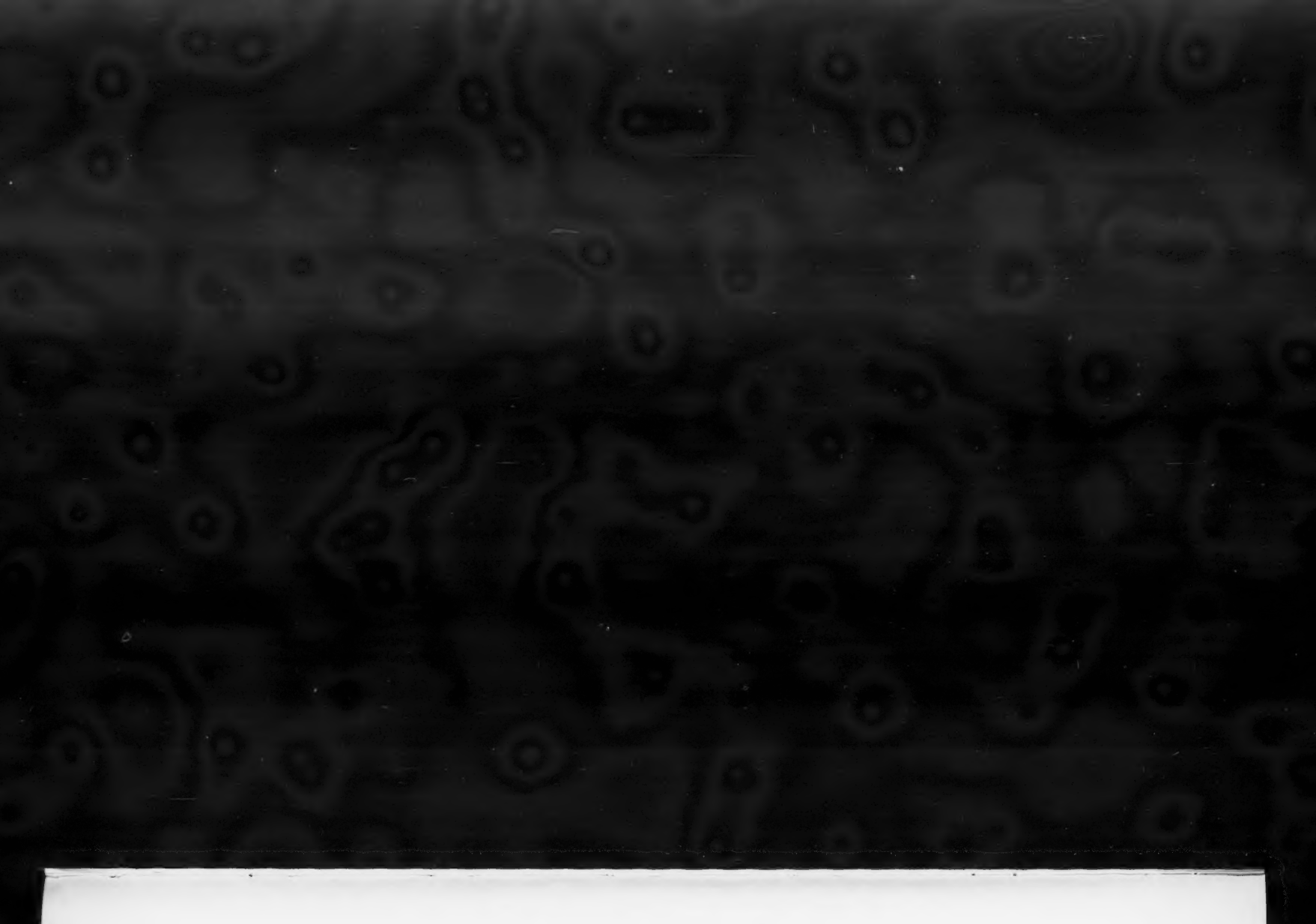
obovate, 7.5–13 cm. long (including the 2–3.5 cm. long petiole), obtuse, apiculate, acuminate into the petiole, sparsely and minutely glandular-denticulate or subentire, evenly but not densely long-pilose above (the hairs whitish, with brownish tuberculate bases, about 4 mm. long), beneath green, similarly pubescent; other stem leaves oblong-elliptic or oblong-ovate to elliptic, 5–7 cm. long, 1.3–2.2 cm. wide, sessile by a broad base, otherwise similar to the lower leaves; chief branches of inflorescence about 5, the lowest subtended by leaves similar to the upper stem leaves, the others by reduced lanceolate or lance-linear bracts 1–4 cm. long, 1–10 mm. wide; panicle loose, 20–48-headed, about 12 cm. wide; pedicels pubescent like the upper part of the stem, 7–17 mm. long; involucre campanulate, 7–8 mm. high in fruit, 2-seriate, equal or subequal, without evident calyculus, the phyllaries lance-subulate, acuminate, blackish-green (the inner with thin pale margins), evenly but not densely pilose with spreading blackish eglandular hairs about 2 mm. long and especially at base pedicellate-glandular, the hairs blackish below, yellowish above like the glands; heads about 43-flowered, the corollas not seen; achenes blackish-brown, 2.2 to 2.5 mm. long, columnar-ovoid, abruptly contracted downward near base, gradually narrowed to apex, not at all beaked, about 12-ribbed, minutely hispidulous especially toward base; pappus brownish-straw-color, fragile, 5.5 mm. long, equaling the involucre.

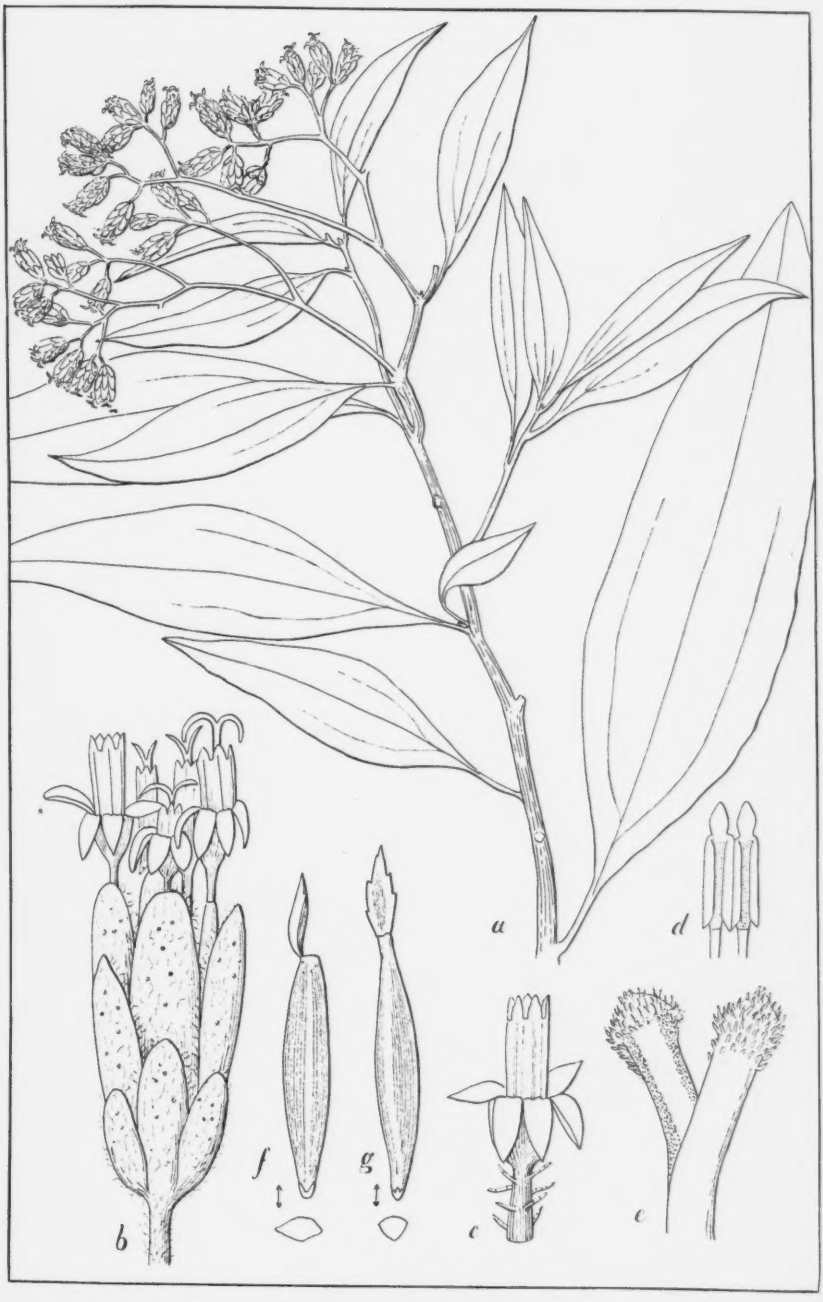
BOLIVIA.—La Paz, March 19, 1920, *E. W. D.* and *M. M. Holway* 425 (type in U.S. National Herbarium no. 1058601).

BUREAU OF PLANT INDUSTRY
WASHINGTON, D.C.

EXPLANATION OF PLATE XIX

Monopholis hexantha Blake.—*a*, branch, ×½; *b*, head, ×8; *c*, disk corolla, ×8; *d*, stamens, ×8; *e*, style branches, much enlarged; *f*, *g*, two achenes in lateral and dorsal view, ×8.





BLAKE on ASTERACEAE

RECENT STUDIES OF PHAEOPHYCEAE AND THEIR BEARING ON CLASSIFICATION

WM. RANDOLPH TAYLOR

Introduction

During the past decade there has been so fundamental an advance in our knowledge of the reproductive processes and life history of the Phaeophyceae, that it seems to exceed in importance the change in viewpoint regarding any other group of plants during the same period. The work which must so largely overturn our ideas has mainly been done by European algologists, and has not been followed up in this country by any confirmatory studies; indeed, it seems to be little known. As each succeeding paper, and several from independent sources have now appeared, confirms the critical points of the others, it seems desirable at this time to review the situation and to indicate the necessary changes in the classification of the group. To date the only review in English of the studies in question is a short one by LEWIS (11), written at an early stage. Three have appeared in France, one by CONSTANTIN (1), and two by PECHOUTRE (16, 17), these latter of special value.

Historical

The pioneer in this field, to whom falls the honor of making the first clear advance, is SAUVAGEAU. Previous to the appearance of the standard texts, he, with other workers, had cleared up the normal life history of *Cutleria*, showing the relation of *Aglaozonia* as the sporophyte stage, and showing the variations in the life history (parthenogenesis, etc.) which appeared under various conditions (18, 19, 22, 23, 24). Further, his studies on members of the Sphacelariaceae and Ectocarpaceae have done much to help in the understanding of those families (20, 21, 33). Most important in the present connection, however, are his results from cultures of Laminariaceae (25–30, 32). In 1910 DREW (2) described the products of the unilocular sporangia on the surface of the *Laminaria*

frond as functioning as gametes, and as producing a somewhat filamentous stage from which the mature *Laminaria* was vegetatively developed. A paper by KILLIAN (5) the following year, in discussing the development and structure of *Laminaria*, agreed, so far as it went, with the statements of DREW. This decidedly unexpected phenomenon of the sexual fusion of what from their origin should be zoospores met with considerable doubt, however, and was attacked by WILLIAMS (37), who claimed that it was not the motile zoospores of *Laminaria*, but other organisms, which had been seen to fuse by DREW. The first of SAUVAGEAU'S papers on the life history of the Laminariaceae appeared as a series on *Saccorhiza bulbosa* (25, 26, 27). Here he showed that in the case of the female the germinating zoospores from the unilocular sporangia produce a one to few-celled filament. The cells of this filament enlarge and emit a non-motile egg, which seemed to be fertilized *in situ* at the aperture, where it developed into a young sporophyte. The male plant is more complex, of five or six cells and slightly branched, with several more or less clustered antheridia. Germination of the zoospores within the sorus in which they were formed was seen, and it was found that the sporelings were both male and female, demonstrating that the sporangia on one plant produced both sorts.

Following this study appeared one on two species of *Laminaria*, *L. flexicaulis* (*L. digitata*) and *L. saccharina* (28, 30). SAUVAGEAU found that in germination the chromatophore of the spore divides (the zoospore on attaching itself rounds up and forms a firm wall), and one half passes into the germ tube as it elongates. The nucleus also divides, and one daughter nucleus with a chromatophore passes toward the inflated distal end of the tube, where it is cut off by a transverse wall. The nucleus which remains behind disorganizes more or less rapidly, while the cell with the other nucleus develops the gametophyte. Some of the male filaments are short, but others are elongate and markedly branched, forming the antheridia laterally on the branches toward the end. One sperm is formed in each antheridium, and the sperms are shed before the female gametophytes in the same culture reach maturity. The female gametophytes are from one to several cells in extent, all

cells being able to form eggs. Each cell swells, elongates, and the egg emerges through a terminal rupture at the end of the protuberance. The opening of the oogonium forms a sheath around the base of the egg, which develops into the young sporophyte while attached to the gametophyte. Actual fusion of the gametes was not observed.

Promptly following the papers on *Laminaria*, SAUVAGEAU published a similar study of *Alaria esculenta*, belonging to a different section of the same family. The gametophytes differed from the previous cases in several particulars. The "embryo spore," or zoospore, which has passed into the resting stage, persists and may give rise to a second filament opposite the first. The gametophytes are also larger, and the female has elongate cells, part of which only seem to produce eggs. The fertile cells form irregular lobes instead of remaining of the usual simple ovoid form, but only one egg is extruded from each cell. Sometimes the female thallus is reduced to a single cell, as is not infrequent in *Laminaria*, but is more often of from two to four cells, with the terminal one becoming fertile first, and then occasionally some of the others.

In the same year that the *Laminaria* and *Alaria* studies of SAUVAGEAU were announced (1916), KYLIN published a paper on an independent study of the life cycle of *Laminaria digitata* which confirmed the statements of SAUVAGEAU in all essential respects (**8**). KUCKUCK (**7**) and PASCHER (**15**) also later published confirmatory accounts of studies on *Laminaria saccharina*. The latter describes a most interesting departure, where he found that occasionally cells of the very young sporophyte, or even the undivided egg, might function as unilocular sporangia producing 2, 4, 8, or 16 zoospores. Finally, IKARI (**4**) described the gametophytes of *Laminaria religiosa*, which are like the two species already studied in most points, but at times have the antheridia in rows at the ends of the branches of the thallus, and shed the sperm by a terminal pore.

In the year following his papers on *Laminaria*, SAUVAGEAU gave an account of the development of *Dictyosiphon foeniculaceus*, which demonstrated another unsuspected type of alternation. The evident plant of *Dictyosiphon* only produces unilocular sporangia.

SAUVAGEAU succeeded in getting good cultures in which the zoospores germinated quickly to form a branched filamentous thallus of considerable extent, reaching a millimeter in diameter and forming hairs. When mature, cylindrical gametangia are formed with two to twelve loculi. Each cell forms a single gamete. The septae disappear before dehiscence, and the isogamous gametes escape by a terminal pore. Conjugation was not observed, but was undoubtedly present, for a part of the rounded up, quiescent cells produced from the gametes had two nuclei and two chromatophores. Germination soon took place, and produced a short filament which in a few weeks gave rise to an erect thallus with the essential structure of *Dictyosiphon*.

It is a matter of peculiar satisfaction that the work of KYLIN (10) definitely shows *Chorda* to have the same sort of life history as *Laminaria*. The vegetative similarities which this genus shows to the kelps are not sufficient alone to place it in the same family, but the demonstration of a precisely similar life cycle removes all question of the relationship. The gametophytes are considerably larger than those of *Laminaria*. KYLIN was able to confirm the cultural studies by some incomplete cytological details. In the vegetative cells of the sporophyte tissue there are present forty chromosomes. Reduction divisions take place in spore formation, and are followed by two vegetative haploid divisions. Good fixation was prevented by the paraphyses, and countable metaphases were not found, but synapsis, diakinesis, and other conditions typical of the first reduction division were recognized. The number of chromosomes was about twenty, although it could not be determined precisely. In addition to the study of the preceding species, KYLIN has given details of at least part of the life cycle of several other genera in other families, which will be discussed in connection with the changes in the classification of those families.

Recently SAUVAGEAU has discovered what he believes to be the gametophyte of *Phyllaria reniformis* in the tissues of *Lithophyllum lichenoides* (32). Finally, there has appeared a preliminary note by WILLIAMS (38) relating to a detailed study of cultures of *Laminaria* and *Chorda*, with descriptions of the gametophytes of these genera essentially as previously outlined. In addition, he men-

tions having observed the fusion of the gametes and even of the gamete nuclei of *Laminaria*, completing the morphological evidence of alternation of generations in that genus.

Classification

It now remains to be seen what effect these recent discoveries will have on our ideas of the grouping of the genera of the brown algae. The standard text on the brown algae to date is that of OLTMANNS (14), published in 1904–1905. The classification used there differs from that of KJELLMAN of 1891 (6) in several features, notably in the reinclusion of the Dictyotales in the Phaeophyceae with the Fucaceae, and in the reduction of several groups of the Phaeosporeae from the rank of families, including them under the Ectocarpaceae. The classification accepted by LOTSY (12) is nearly that of OLTMANNS. A recent table by SCHAFFNER (34) disregards all the more recent discoveries, giving four orders in the Phaeosporeae: Ectocarpales (isogamous), Laminariales (zoospores only), Cutleriales (anisogamous), and Tilopteridales (oogamous). In the Cyclosporeae he includes Fucales and Dictyotales. The obvious fact that only a small proportion of the genera known have been fully studied, and even that some families are only understood in the most fragmentary fashion, need not deter us from taking full advantage of the knowledge which is at hand. It must also be borne in mind in all cases that parthenogenesis and other kinds of short cuts in the life cycle may be present, and may be so characteristic of the ordinary propagation of the plant that the fundamental type of alternation upon which the classification is based may be obscured.

The orthodox division into two major groups, Phaeosporales and Cyclosporales, is still acceptable, provided the former is understood to include anisogamous as well as isogamous forms, and a widespread morphological alternation. The Cyclosporales include all oogamous groups, and may show a reduction from a morphological to a mere cytological alternation of generations. The first division of the Class PHAEOPHYCEAE is then the

Order PHAEOSPORALES.—This may be defined as having gametes isogamous to anisogamous. It includes three suborders, as follows:

Suborder ECTOCARPINEAE.—Morphological alternation of similar generations shown or inferred to be present.

Family 1. *Ectocarpaceae.*—Reproductive organs formed by the metamorphosis of all or part of a branch; growth of the free filaments intercalary. This is the primitive family of the class. In *Ectocarpus* the fusion of the elements from the plurilocular sporangia as gametes has been known since the work of BERTHOLD. Recently KYLIN (10) has reviewed the work on *Ectocarpus*, and contributed a study of two species, *E. siliculosus* and *E. tomentosus*. It is to be considered that the plants with sporangia (unilocular) and those with gametangia (plurilocular) normally alternate in the life cycle. Cases of abbreviation of this are well known, and peculiar conditions, as in *E. Padinae* Sauv., have been reported (33). The thallus is always primitively branching-filamentous, and intercalary growth is typical, but this becomes localized in some species into definite regions, while the hapteron branches and other attached or endophytic parts grow apically. These features are of importance as indicating the source of similar characters in the following families.

Family 2. *Tilopteridaceae.*—Reproductive elements of two kinds, small motile cells which may function as isogametes, and larger non-motile cells often with more than one nucleus. These latter cells are of two kinds according to some accounts, representing eggs without a membrane and but one nucleus, and monospores with a membrane and usually four nuclei. The oogamous character of this family has long been tentatively accepted, but has never been proved absolutely. On the basis of vegetative characters and an assumed isogamy, this family would stand in close relationship to the Ectocarpaceae, but if oogamy is actually present it would need to be placed in the Cyclosporales as a suborder Tilopteridineae preceding the Dictyotinieae, differentiated by the thallus characters and the incomplete division of the spores. For a discussion of literature see KYLIN (9).

Family 3. *Sphacelariaceae.*—Reproductive elements formed by the metamorphosis of all or part of a branch, growth from an apical cell. The originally monosiphonous filament usually divides up by internal walls, and may develop a peripheral meristematic zone producing a very considerable increase in thickness. Special vege-

tative methods of reproduction are present in most forms. SAUVAGEAU (**20**) reports finding egg and sperm production on one individual of *Halopetris scoparia*, but could only find one type of gametangium in *Cladostephus*. If this observation is confirmed, it will either force *Halopetris* into the Cyclosporales, a removal of the whole family from its present position, or necessitate a wider interpretation of the Phaeosporales. The family as understood here includes the Choristocarpaceae of KJELLMAN.

Family 4. *Asperococcaceae*.—Reproductive organs formed by the metamorphosis of, or as an outgrowth from, a superficial cell; growth intercalary. This family corresponds to the Encoeliaceae, Striariaceae, and Myriotrichaceae of KJELLMAN, the latter two representing simpler forms with the same essential construction. Plants are derived from a simple filament, becoming parenchymatous, either cylindrical or flattened. All stages can be traced. Gametangia with isogametes and sporangia are present, and considerable portions of the life history are known, especially of *Asperococcus* and *Scytosiphon* (**10**). The statement of YENDO (**43**) that the products of the plurilocular sporangia of *Phyllitis* are not gametes, but give rise to a microscopic gametophyte, requires confirmation.

Family 5. *Chordariaceae*.—Thallus differentiated into axial and assimilative filaments, branched, meristem localized; sporangia replacing assimilative filaments or modified segments therefrom. Essentially filamentous, the final short branches of the axial filaments turn outward and form a close cortex rich in chromatophores. Since both sporangia and gametangia are known in these genera, the life history is probably the same as that of *Ectocarpus*. The Elachisteaceae of KJELLMAN represent a reduced epiphytic group, and may best be included in the Chordariaceae.

Family 6. *Desmarestiaceae*.—Reproductive organs formed by the metamorphosis of, or as an outgrowth from, a free (or corticating) branch cell; growth trichothallic. The main axis in these forms is ramified, and produces short corticating branches, as well as (in some) delicate free ones. Little is known regarding the development of these genera; unilocular sporangia only are present, and there may be the same life history as in *Dictyosiphon*.

Family 7. *Stilophoraceae.*—Reproductive organs lateral on special branched supports, thallus erect on the substratum. As understood here, this family includes KJELLMAN'S Stilophoraceae, Spermatochnaceae, and Sporochnaceae. The sporangia are borne on branched filaments developed from superficial cells of the thallus, and both sporangia and gametangia are known. Parts of the life cycle have been traced by KYLIN (10).

Family 8. *Ralfsiaceae.*—Reproductive organs at least in part lateral on special branched supports, thallus incrustating. Here we may include with the Ralfsiaceae also KJELLMAN'S Lithodermataceae. In both the gametangia are borne laterally on special branched filaments arising from the surface, but the sporangia are only so borne in the Ralfsiaceae, in *Lithoderma* being but modified surface cells. The life history is unknown from the experimental viewpoint.

Suborder DICTYOSIPHONINEAE.—Morphological alternation of dissimilar generations present or inferred, the sporophyte exceeding the gametophyte in size.

Family *Dictyosiphonaceae.*—Characters of the suborder. The forms are branching, have an apical cell, and differentiate axial and cortical areas. The life history, worked out by SAUVAGEAU (31), has previously been described. This is a very important group, as it indicates an intermediate step in the development of a microscopic oogamous thallus, such as is shown in *Laminaria.*

Suborder CUTLERINEAE.—Morphological alternation of similar or of dissimilar generations present, gametophyte when different larger than the sporophyte; growth trichothallic.

Family *Cutleriaceae.*—Characters of the suborder. The life history of this group is well known, thanks to the cultural studies of SAUVAGEAU, CHURCH, and several others, and to the cytological studies of YAMANOUCHI on *Cutleria* (40, 41) and *Zanardinia* (42). The alternation shown by the cultural studies has been shown to be associated with a haploid and diploid nuclear constitution, reduction taking place in the sporangia. In *Zanardinia* the two generations are essentially alike, but in *Cutleria* the reduced and flattened sporophyte was long known as *Aglaozonia*, and thought to be an entirely different genus.

Order CYCLOSPORALES.—Plants of this order are strictly oogamous.

Suborder DICTYOTINEAE.—Morphological alternation of similar generations present.

Family *Dictyotaceae.*—Characters of the suborder. The gametangia are aggregated into definite areas or sori, and the asexual reproduction is by tetrasporangia, motile zoospores being replaced by four non-motile elements. The life cycle of *Dictyota* is fully known. Cultural studies showing the course of the development have been made by HOYT (**3**), and cytological studies by MOTTIER (**13**) and WILLIAMS (**35, 36**), showing reduction in tetraspore formation.

Suborder LAMINARINEAE.—Morphological alternation of dissimilar generations present, gametophyte smaller than the sporophyte.

Family *Laminariaceae.*—Characters of the suborder. Members of this family are almost all large plants. Reproduction was thought to be strictly by zoospores until SAUVAGEAU showed that the zoospores produced a microscopic gametophyte. The results of the various studies have previously been described.

Suborder FUCINEAE.—Only cytological alternation of generations present.

Family *Fucaceae.*—Characters of the suborder. This family forms the spores within pits or conceptacles. Still inclosed, the spores undergo a few cell divisions, or even only a few nuclear divisions, forming the gametes which are then shed as egg and sperm. Cytological studies have been made by several workers, including YAMANOUCHI (**39**), confirming the morphological and cultural observations. This is the climax family of the brown algae, and represents the greatest reduction of the gametophyte possible while still retaining an alternation.

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A METHOD FOR ESTIMATING HYDROPHILIC COLLOID CONTENT OF EXPRESSED PLANT TISSUE FLUIDS[1]

ROBERT NEWTON AND ROSS AIKEN GORTNER

(WITH ONE FIGURE)

In the preceding paper by GORTNER and HOFFMAN[2] it was pointed out that studies of the physico-chemical properties of plant saps which include only measurements of the osmotic pressure, electrical conductivity, and H-ion concentration, leave out of account the very important influence on physical properties exerted by sap colloids. By the introduction of the refractometer as a part of the field laboratory equipment, these workers have shown it possible to make rapid and accurate determinations of the moisture content of the plant saps. Utilizing the additional data thus made available, a simple method has been devised which appears to give a relative measure of the content of hydrophilic colloids.

The freezing point depression of the freshly expressed plant juice is first obtained. Then, having determined the total solids by the refractometric method, a quantity of sucrose just sufficient to make a molar solution in the total water present is added. The freezing point depression is again determined, and is usually found to have increased more than the theoretical amount.

The values for the excess depression recorded in this paper have been based on the assumption that sucrose forms the hexahydrate in solution. The evidence for this has recently been discussed by SCATCHARD,[3] who also contributed additional data. In preliminary experiments with pure sucrose dissolved in distilled water, freezing point depressions were obtained slightly in excess of those

[1] Published with the approval of the Director, as Paper no. 323, Journal Series, Minnesota Agricultural Experiment Station.

[2] GORTNER, R. A., and HOFFMAN, W. F., Determination of moisture content of expressed plant tissue fluids. BOT. GAZ. 74:308–313. 1922.

[3] SCATCHARD, G., The hydration of sucrose in water solution as calculated from vapor-pressure measurements. Jour. Amer. Chem. Soc. 43:2406–2418. 1921.

expected under this assumption, but it is preferred to use the theoretical value until further data on this point are available.

It is assumed that the magnitude of the excess depression is a measure of the quantity of water held in such a way as to be unavailable for the solution of the sugar. The values obtained may be calculated to percentage "bound" water. This represents the total water of hydration of all the substances in the sap, but has been found to correspond so regularly with the content of hydrophilic colloid as to indicate a close relationship. It seems probable that in most cases the water bound by substances other than colloids is of minor importance.

In table I are reported the data for a number of the samples of expressed juice included in table I of the preceding paper, and in addition for a series of gum acacia sols prepared by weighing out the necessary quantities of highly purified gum acacia and distilled water. The percentage of total solids, as read directly by the refractometer, is given in column 2. The values for viscosity, recorded in column 3, were determined by a viscosimeter of the Ostwald type, in a constant temperature bath at 25° C.; the figures are the number of seconds required for 3 cc. to flow through a capillary tube, through which the same quantity of distilled water flowed in 204 seconds. In column 4 is given Δ, the freezing point depression of the freshly expressed juice; in column 5 Δ_a, the freezing point depression after the addition of the sugar; in column 6 $\Delta_a - \Delta$, the actual additional depression due to the added sugar; in column 7 $\Delta_a - (\Delta + K_m)$, the amount by which the depression found on addition of the sugar is in excess of that expected on theoretical grounds. As previously noted, it has been assumed that sucrose forms sucrose hexahydrate in solution, and therefore K_m, the molecular constant for the depression of the freezing point, has been taken as 2.085° C. instead of the usual 1.86° C. The percentage "bound" water, given in the last column of the table, is conveniently calculated from the value for actual additional depression due to the added sugar ($\Delta_a - \Delta$). The calculations involved will be made clear in the following example, using the first item in the table.

$1.86° = \Delta$ due to 1 mole dissolved in 1000 gm. water, but 1 mole sucrose combines with 6 moles water. Thus 1 mole sucrose dis-

solved in 1000 gm. water = 1 mole sucrose hexahydrate dissolved in 1000 − (18 × 6), or 892 gm. water, and 2.085° (K_m) = Δ due to 1 mole dissolved in 892 gm. water.

But in sample 13 the increase in Δ on addition of 1 mole sucrose ($\Delta_a - \Delta$) was 2.339°, and 2.339° = Δ due to 1 mole dissolved in $\frac{1.86 \times 1000}{2.339} = 795$ gm. water; therefore the water bound per liter = 892 − 795 = 97 gm., = 9.7 per cent.

In laboratory practice it is most convenient to weigh out a fresh portion of the sap containing 10.0 gm. of water, add 3.422 gm. of sucrose, and redetermine the freezing point. The percentage of bound water is then given by the formula: $\frac{\text{Excess } \Delta}{\text{observed } \Delta - \text{sap } \Delta} \times 892$ or bound water $= \frac{\Delta_a - (\Delta + K_m)}{\Delta_a - \Delta} \times 892$.

Comparing sample 13 with sample 16, it will be seen that whereas the percentages of total solids vary widely, the percentages of bound water are not greatly different. A reference to the values for viscosity and Δ will indicate at once the marked difference in the physical properties of these two saps, due to the large content of colloidal material in sample 16, a fact which is strikingly reflected in the percentage of bound water. Again, dialysis showed that material similar to sample 17 contained approximately twice the quantity of colloids as was contained in material similar to sample 20, and these two samples differ widely in percentage bound water. These examples are cited to illustrate the application of the method. Discussion of the significance of the variations observed in the wheat varieties is reserved for a later paper on another subject.

The percentages of bound water obtained with gum acacia sols, as shown in the table, increase regularly with concentration. In fig. 1 the percentage concentration has been plotted against the percentage bound water. The logarithms of these values have also been plotted in the same figure. It will be seen that both of these graphs suggest an adsorption curve.

The advantages of sucrose as the solute in this method are as follows: (1) it is easily obtained in a high degree of purity; (2) the large molecular weight reduces errors in weighing; (3) its behavior

TABLE I

Materials used: leaves of	Total solids	Viscosity (water = 204)	Δ	Δ_a	$\Delta_a - \Delta$	$\Delta_a - (\Delta + K_m)$	Bound water
	Per cent	seconds					Per cent
13. Triticum vulgare var. Turkey	13.5	360	1.273	3.612	2.339	0.254	9.7
15. Bryophyllum calycinum	5.9	235	0.474	2.555	2.081	−0.004	0.0
16. Cereus sp	4.9	637	0.505	2.803	2.298	0.213	8.3
17. Triticum vulgare var. Buffum	17.8	419	1.719	4.158	2.439	0.354	13.0
18. Triticum vulgare var. Minhardi	8.5	285	1.147	3.824	2.137	0.052	2.2
19. Triticum vulgare var. Super	7.1	267	1.000	3.106	2.106	0.021	0.9
20. Triticum vulgare var. Super	9.7	292	1.085	3.279	2.194	0.109	4.4
Solutions of gum acacia							
1 per cent	1.0	309	0.005	2.147	2.142	0.057	2.37
3 per cent	3.0	487	0.013	2.186	2.171	0.086	3.53
5 per cent	5.0	684	0.025	2.221	2.196	0.111	4.50
7 per cent	7.0	932	0.034	2.254	2.220	0.135	5.42
10 per cent	10.0	1438	0.048	2.294	2.246	0.161	6.39

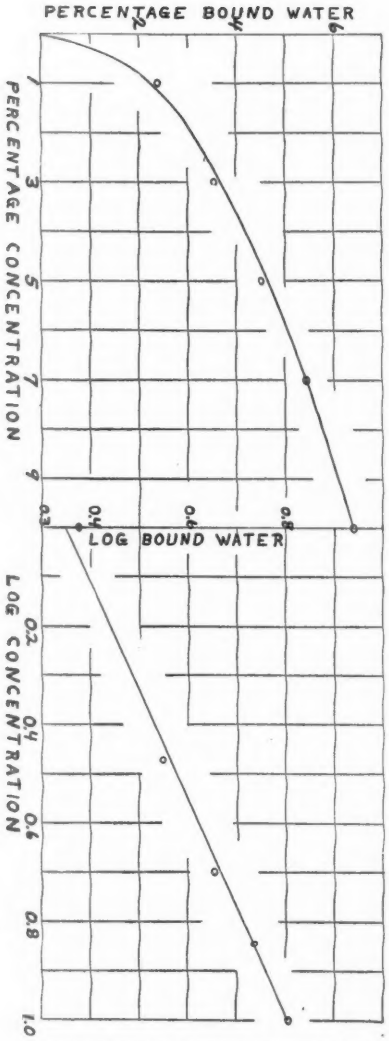

FIG. 1.—Relation between concentration of gum acacia sols and water bound by the colloid.

in solution is fairly well known; (4) its effect on the swelling of colloids is probably negligible. In objection it may be stated that plant saps probably contain invertase, but the plan has been followed of grinding the sucrose to a fine powder which dissolves rapidly with shaking, and the sap has been maintained continuously at low temperature. Under these conditions no increased depression of the freezing point which could be attributed to invertase action has been observed in a somewhat extended series of determinations on the same sample.

Conditions of equilibrium, and possible errors due to adsorption of the sugar by colloids, have not yet been investigated. The data already secured, however, appear to justify the proposal of the method for the estimation of the relative (not absolute) content of hydrophilic colloids in expressed plant tissue fluids. It seems probable that the method may be applied also to other biological fluids.

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GROWTH OF PLANTS IN ARTIFICIAL LIGHT

R. B. HARVEY

(WITH TWO FIGURES)

The growth of plants in artificial light has been of interest in plant physiology because it offers the possibility of controlling the quality and intensity of the light, and the duration of the exposure. No reliance can be placed upon sunlight, and its quality and intensity vary greatly. The writer attacked the problem of growing plants in artificial light to gain some idea of the relation of light intensity to the formation and equilibrium concentrations of the carbohydrates formed in leaves, and to the translocation of these substances in light and darkness.

The problem of producing plants in artificial light is of some economic interest in Minnesota and other such localities, where the sunlight is of short duration and low intensity in winter. It is difficult to raise plants in the greenhouse in winter in this latitude when the sun is at a low angle. Some analyses made on cabbage leaves grown in a greenhouse at the University of Minnesota in the winter of 1920 show a practical absence of sugars from the leaves. Very little growth is produced under such conditions; the plants are weak and easily attacked by fungi.

The ability to grow plants in this climate by substituting artificial light for sunlight, or by using artificial light to supplement sunlight on dark days, will be of considerable value for plant breeders. The progeny of valuable crosses can be carried through one or more generations during the winter, and thereby decrease the time required to produce a new strain. In breeding for rust resistance at Minnesota it has been found difficult to carry biological forms of black stem rust of wheat in culture during winter, owing to the weakness of the host plants.

The writer has succeeded in raising a great variety of plants from seed to maturity, using artificial illumination entirely. Light was obtained from nitrogen-filled tungsten filament (Mazda) lamps. The lamps were mounted on the ceiling of basement rooms

about five feet from the plants. Ordinary enamelled reflectors of the deep bowl type were used to throw the light downward. The lamps used were of the 200 watt and 1000 watt sizes; the latter is considerably more economical in operation than the smaller size. These lamps are rated to burn 1000 hours, but average about 3000 hours. They were burned twenty-four hours per day, so that one set of lamps was sufficient for four months or more. Breakage of the lamps occurred the most frequently when the current was turned off and the filaments allowed to cool. The continuous burning seemed to greatly increase the life of the lamps.

Plants grew well, set good seed or produced tubers in the continuous illumination. It seems unnecessary to have a period of darkness to allow translocation of the assimilate from the leaves. Several intensities of light were used and the plants grew in each. The lowest intensities of about 25 foot candles in dark corners produced much better growth than was obtained in the greenhouse during the winter. Analyses of the carbohydrate and protein contents of the plants are being made.

In one room 8×11 feet a great variety of cereals was grown, including twenty varieties of wheat, fifteen varieties of oats, eighteen varieties of barley, eight varieties of rye, six varieties of flax, several hybrids of wheat and of oats, and a few other test plants. The room was lighted by lamps with a total capacity of 3200 watts and distributed uniformly. The lamps required about 0.6 watt to produce one spherical candle. Then $\frac{4\pi \times 3200}{0.6} = 67{,}021$ lumens total flux. On account of the light absorption and inefficiency of the reflectors, only about 60 per cent of this light reaches the ground, so that there are 40,212 lumens spread over the area 8×11 feet, giving an intensity of about 457 lumens per square foot. In this light winter rye headed at about 24 inches; Kota wheat at 28 inches; Bluestem wheat at 23 inches; Aurora oats at 17 inches; Manchuria barley at 17 inches. These plants were grown in 5-inch pots. Usually six or eight kernels were all that set in a head of wheat, but these were plump and full of starch. The temperature was maintained automatically at about 14° C. by cooling with outside air. It was unnecessary to use any heat in this room other than that produced by the lights. The light is doubly

efficient, for all that is not used by the plants goes to heat. Since sunlight is not required, the rooms can be insulated much better against heat loss than a greenhouse.

In a room 6×11 feet, lighted by 10–200 watt lamps, several vegetables were grown. The temperature was about 25°–30° C., not well controlled. The light intensity was about 380 lumens per square foot. Potatoes and tomatoes grew well, but were somewhat taller than normal. Early Ohio potatoes bloomed when the vines

FIG. 1.—Cabbage, lettuce, potato, tomato, beans, peas, and a number of other plants growing in continuous artificial light; room 6×8 feet, lighted with lamps of 2600 watts capacity.

were 44 inches long. Boston marrow squash bloomed at 42 inches, but did not set fruit. Alaska peas bloomed at 18 inches and set good seed. *Solanum niger* set abundant fruit, beginning at 6 inches, and continued fruiting up to 28 inches. Cabbage started heads at about 18 inches and showed some effects of etiolation. Buckwheat set normal seed at 20 inches.

In another room 6×8 feet, lighted by lamps with a total capacity of 2600 watts, the plants appeared much more normal than in the room just mentioned (fig. 1). The light intensity here was about 680 lumens per square foot and the temperature 25°–30° C. Cabbage

headed at 12 inches; lettuce set abundant seed when 36 inches high. Black wax beans set pods at 35 inches; potatoes (Early Ohio)

FIG. 2.—Rotating tables operated by electric phonograph motor to equalize light and temperature.

bloomed at 48 inches, and set tubers weighing as high as 180 gm. each. White sweet clover set some seed when 40 inches high. A number of weeds were allowed to grow, and they all set abundant seed. *Boltonia asteroides* bloomed when 54 inches high; *Chenopodium ambrosioides* set seeds profusely at 35 inches; *Silene latifolia* bloomed at 16 inches but did not set seed; *Stellaria media* bloomed and set seed at 16 inches; foxtail grass (*Alopecurus*) set abundant seed at normal height.

Under the 1000 watt lamp shown in fig. 2 the light intensity was about 4188 lumens per square foot. Plants under this light were very stocky, and showed effects of too much heat. The leaves of cabbage were very turgid and stiff. The plants were rotated to equalize light and temperature, and to decrease the heating effect of the light on surfaces directly exposed.

All of the plants in these rooms except cabbage bloomed, and many produced good seed, although the illumination was continuous. It seems then that the period of illumination is not the factor which determines whether a plant will bloom or not. The results obtained by GARNER and ALLARD[1] may have been produced by a modification of the conditions of nutrition of their plants by variation in the length of the day. It is possible to obtain seed from a great variety of plants as here shown, although the illumination is continuous, and the intensity is approximately the same for all plants in one room.

Summary

A great variety of plants, including wheat, oats, barley, rye, flax, buckwheat, white sweet clover, peas, beans, lettuce, and a number of common weeds were grown from seed to maturity in continuous artificial light, and all set good seed. Potatoes, tomatoes, red clover, alsike clover, squash, and *Silene* bloomed, but did not set seed. Potatoes produced tubers of good size. All of the plants tested did not require a certain period of illumination to cause them to bloom. It is possible to produce seed from plants in winter independent of sunlight, and at no very great expense.

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[1] GARNER, W. W., and ALLARD, H. A., Jour. Agric. Res. 18:553–606. 1920.

CURRENT LITERATURE

MINOR NOTICES

North American slime moulds.—A new and revised edition of MACBRIDE'S[1] *North American slime moulds* has just been published. As the subtitle states, it is "a descriptive list of all species of Myxomycetes hitherto reported from the continent of North America, with notes on some extra-limital species." The original edition was reviewed in this journal.[2] The necessity for a second edition has given the author the opportunity not only to correct certain errata, but chiefly to incorporate new information developed by the investigation of the last twenty years. The book is primarily for American students, and is certainly an adequate presentation of this interesting group, serving the same purpose in this country that LISTER'S *Mycetozoa* does in England.—J. M. C.

Some elementary texts.—An interesting textbook for Indian high schools has been prepared by KENOYER.[3] It is interesting both in presentation and material, and adapted to high school students of India. Of course it is necessarily brief, but it develops an interesting approach to the plant kingdom. It is based upon the conviction that the best way to know plants is to grow them, and therefore emphasis is placed upon the school garden as the important laboratory for beginners. The plants selected as illustrations are in general those of general occurrence in India. This little book will interest teachers of botany in other countries.

A similar text for English schools has been prepared by WOODHEAD.[4] This is an abbreviation and simplification of the author's *The study of plants*. It also emphasizes the study of living material, experimental work, and outdoor observation. Naturally the materials are those available in England, and the details and terminology are more technical than in the Indian text. Both are doubtless adaptations to the status of high school education in the two countries.—J. M. C.

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[1] MACBRIDE, T. H., The North American slime moulds. 8vo. pp. xvii+299. *pls. 23*. New York: The Macmillan Company. 1922.

[2] BOT. GAZ. **29**:74. 1900.

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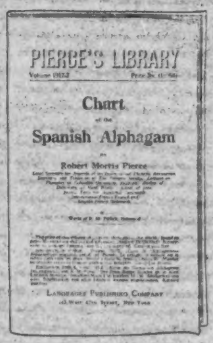

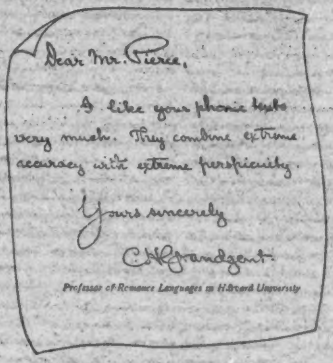
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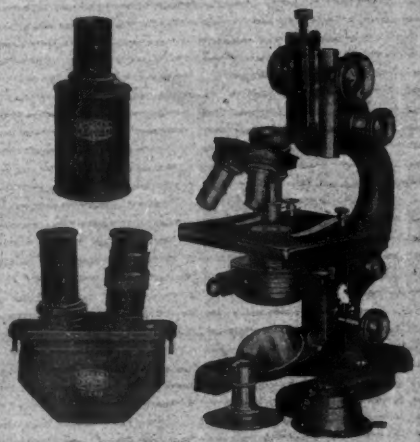

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